Habitat Use and Trophic Ecology of Bronze Whaler Sharks (*Carcharhinus brachyurus*) in New Zealand

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Abstract

Sharks are among some of the most diverse and abundant top-level predators within marine ecosystems. Their predatory role in controlling the population size, distribution and behaviour of species within the lower levels of the food web make them an integral component in both coastal and oceanic communities. However, anthropogenic pressures are causing declines in many shark populations across their range, with the ecological consequences following the removal of top predators from marine communities yet to be fully understood. Insight into the dynamics of shark ecology is further complicated by the heterogeneity of variables regulating natural communities. Despite this, research on trophic cascades, and the direct and indirect effects of apex predators on successive levels of the food web has been achieved where top-level predators have been removed from systems.

As a consequence of the difficulty in researching elusive species such as sharks in the marine environment, an understanding of the biology and ecology of many species remains limited. However, such information is critical if effective decisions on the management of shark species and the wider marine environment in which they interact, are to be made. Although considered common, the bronze whaler shark (*Carcharhinus brachyurus*) remains relatively unstudied. Found in warm temperate environments, this species is known to utilise coastal habitats during the summer months. However, little is known about their movements during the winter months when sightings and interactions with fishermen in nearshore waters cease. Using satellite-linked smart position or temperature transmitting (SPOT5) tags and stable isotope analysis, this research aims to investigate the habitat use and trophic ecology of bronze whaler sharks to establish their role as top-level predators within coastal New Zealand waters. This research further aims to build on current knowledge to ensure sound management decisions regarding this species, and to understand the possible ecological community effects if these predators are removed from local marine systems.

Satellite telemetry has revolutionised the way in which scientists track highly mobile vertebrates, and continues to expand our understanding of the behaviour and distribution patterns of shark species across a range of environments and geographic scales. This study provides the first report of the use of satellite tags on bronze whaler sharks. Two mature female bronze whaler sharks were tagged with satellite-linked

smart position or temperature transmitting (SPOT5) tags at the entrance to the southern Tauranga Harbour, New Zealand. Sharks were tagged during April, the beginning of the austral autumn, and tracked for up to 157 days until transmissions ceased towards the end of winter in September. While transmission periods were comparable to those found throughout the literature, transmission rates were low which could be a factor of the surfacing behaviour of this species. However, location accuracies exceeded those of other studies, providing viable tracks for analysis for both sharks. Movement and recapture data indicated a high level of residency and site fidelity to habitats within the north-eastern region of the North Island, New Zealand, suggesting bronze whaler sharks play an important top-down predatory role in structuring the food web dynamic in this region. This also indicated the potential for multiple segregated populations within New Zealand waters. Furthermore, a behavioural shift was evident with the onset of winter, with both sharks moving from inshore and shelf habitats during autumn, to primarily shelf-edge and oceanic habitats during winter. This movement coincided with a decline in coastal water temperatures below 15.1°C. The cessation of transmissions, likely due to biofouling, prevented the identification of a return migration to coastal environments the following summer. However, the data provided new evidence of the importance of shelf-edge and oceanic habitats to this species. Further understanding of their seasonal movements and feeding ecology would enhance our understanding of how their predatory influence may change across seasons and in turn, the implications for inshore and offshore prey assemblages.

Stable isotope analysis presents an alternative method to track the movements and ecology of species, providing information of species interactions and trophic dynamics that cannot be determined through satellite tagging alone. This study examined stable isotope signatures $\delta^{13}C$ and $\delta^{15}N$ of muscle tissue of bronze whaler sharks in comparison with coastal and offshore teleost, invertebrate and algal species from the Bay of Plenty, New Zealand. A total of 40 bronze whaler sharks were caught from the Tauranga coastal region, ranging in length from 236–305 cm total length across the dorsal surface with the tail in a flexed position. Based on previous length at maturity studies, sharks in the data set were considered mature. Out of the 40 sharks captured, only two were male, supporting sex segregation in this species, and a strong association of females to inshore sites. Stable isotope analysis did not detect a change in $\delta^{13}C$ and $\delta^{15}N$ values with increasing length, informing that once bronze whaler sharks reached maturity, they fed off a similar food web and at a similar trophic level. A Bayesian

mixing model was applied to estimate the contributions of potential prey species to the diet of bronze whaler sharks. The model identified kingfish as the most dominant prey source (mean = 50.7%), followed by piper (mean = 11.5%) which indicated the utilisation primarily of a coastal pelagic food web. Snapper also showed to be an important component, indicating trophic links also extended to reef and benthic habitats. The lack of a viable pelagic baseline signature prevented the ability to accurately calculate the trophic position of bronze whaler sharks. However, an examination of bivariate data from all species collected suggest a trophic position between 4 and 5, which was consistent with trophic position estimates previously calculated for bronze whaler sharks and other shark species of a similar size.

This study adopted a multidisciplinary approach to investigate the movement patterns and trophic ecology of bronze whaler sharks captured from coastal sites within the Bay of Plenty. The use of stable isotope analysis can be a powerful tool to complement satellite tracking studies. However, in this case, each technique provided a somewhat contradictory result. It is evident that the ecology of this species is complex, with a larger, more diverse sample size over greater spatial and temporal scales required to further elucidate the many questions still pending over its habitat use and foraging behaviour. Such information is crucial if we are to fully understand the ecological role this species plays as a top-level predator within local marine communities, and its implications for the wider management of valuable ecosystems and fisheries within the region.

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Dedication

This thesis is dedicated to my grandparents, Les and Nola Taylor.

I am the person I am today because of you.

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General Introduction

1.1 Introduction

Apex predators are an integral component of the ecology of both aquatic and terrestrial ecosystems. With few natural predators, they occupy the highest trophic tier with their role in structuring food webs through direct predatory effects, along with indirect influences of intimidation, controlling population size, distribution and behaviour of prey species below them. Sharks are considered to be some of the most diverse and abundant apex predators within marine ecosystems (Ferretti et al., 2010; Roff et al., 2016). However, globally shark numbers continue to be in decline due to a combination of anthropogenic effects, reducing species populations across their range. The consequences of large-scale loss of top predatory species from marine ecosystems is beginning to be understood. Nonetheless, it is difficult to identify ecological perturbations and manage species when knowledge on species abundances, distributions and food web interactions is limited. This information is crucial to ensure the correct management and protection of not only shark species, but also in making decisions for the wider marine environment in which they play a vital role. This thesis aims to elucidate such information on the relatively understudied bronze whaler shark (*Carcharhinus brachyurus*) in New Zealand waters. Using satellite tagging and stable isotope analysis, the spatial and temporal movements, along with trophic interactions of this species were examined and are reported in the following three chapters.

1.2 Sharks (Sub-class Elasmobranchii; Sub-division Selachii)

Sharks are members of the class Chondrichthyes, being characterised by their peripherally mineralised cartilaginous skeleton and the modification of the pelvic girdle to form claspers (mixopterygia) in males (Grogan & Lund, 2004). Such features are important in separating them from the class Actinopterygii, or bony fish. Further taxonomic division separates Chondrichthyes into two sub-classes – Elasmobranchii (sharks, rays, skates and sawfish) and Holocephali (chimaeras). Selachii is the group referred to as sharks and are the focus of this thesis. Cartilaginous fish date back to the

Early Devonian around 400 million years ago (mya) (Cox & Francis, 1997), and have survived all mass extinctions of their time (Grogan & Lund, 2004). Modern sharks, as we see them today, evolved from their more archaic counterparts during the Upper Jurassic, some 150mya, and have remained dominant predators within the marine environment for the last 140 million years (Cox & Francis, 1997). Anatomical innovations such as paired fins, streamlined bodies, flexible tail and an underslung lower mandible (Cox & Francis, 1997; Klimley, 2013), along with their specialised physiology and attuned senses, have ensured their evolutionary success within ocean environments. These features have facilitated their circa-global expansion and diversification into the 494 shark species reported today (www.iucnredlist.org, accessed 14 April 2020).

However, shark populations are declining due to pressures from industrial scale fishing, habitat destruction, coastal development, pollution and climate change, resulting in the reduction of some top predator populations by over 90% (Myers & Worm, 2003), and the extirpation of some species from large parts of their range (Simpfendorfer et al., 2011). Large coastal species have been identified as being most vulnerable as they are more exposed to the combined threat of anthropogenic influences (Dulvy et al., 2014). Furthermore, the life history traits of sharks such as slow growth, late maturity, long gestation periods, small litters and a long inter-birth interval results in low population growth and a limited ability to recover from population declines (Garcia et al., 2008; Dulvy et al., 2014). Although 34.41% of shark species are listed at a level of 'Least Concern' on the IUCN Red List, 16.6% are defined as 'Vulnerable', 'Endangered' or 'Critically Endangered' with 11.13% listed as 'Near-Threatened' (www.iucnredlist.org, accessed 14 April 2020). However, one of the most concerning categories is the 37.85% of shark species that are listed as Data Deficient. The lack of information on the life history traits of these species creates uncertainty when assessing what habitats may be critical to ontogenetic behaviour and the broader sustainability of species populations.

1.3 Habitat use

The circa-global radiation of sharks has resulted in their expansion into a range of habitat types such as deep-sea, oceanic, neritic, estuarine and in some cases, freshwater environments (Simpfendorfer & Heupel, 2004), with temperature and depth being defining parameters in the different geographical distributions of species. With

increasing body size comes the tendency for large predatory species to undergo broader movement patterns (McCauley et al., 2012). Within these environments, smaller sized species (<100 cm TL) typically have a smaller home range compared to larger species (>300 cm TL), the latter being wide-ranging and depending on the species, often have transoceanic scale movements (Musick et al., 2004). Within their range, species often show preferences to particular areas of available habitat, with finer scale niche partitioning being determined by feeding and propulsive specialisations (Grogan & Lund, 2004), distribution of predator and prey species, reproductive activity, and tolerances to physical conditions such as temperature and salinity (Simpfendorfer & Heupel, 2004).

Within species, variations in the use of particular habitats can also occur with ontogenetic development. The importance of estuaries in the life histories of predatory species such as sharks has been well documented (as outlined in Harasti et al., 2017). With high prey abundances and seasonally warmer waters, it is thought that shallow nearshore waters such as estuarine systems provide suitable habitat for nurseries for a number of coastal shark species (Knip et al., 2010). Furthermore, nursery areas provide neonates protection from predators such as larger sharks (Simpfendorfer et al., 2005), and can be utilised by more than one species, although they may be separated by space and time (Heithaus, 2007). However, nursery areas are not just limited to coastal areas, with some species utilising open ocean habitats as nursery grounds. Whilst there is less competition for food in the open ocean for developing young, they are met with the trade-off of greater exposure to predation (Heithaus, 2007). As juveniles increase in size and predation risk decreases, young sharks progressively expand their range to meet increasing energetic dietary requirements as they are recruited into the adult population (Heithaus, 2007). Such an ontogenetic transition was demonstrated in a study by Heupel et al. (2004), who reported expansion in the home ranges of juvenile blacktip sharks (*Carcharhinus limbatus*) during foraging activity from a restricted core refuge in the weeks and months following parturition. Similar shifts have also been observed in lemon sharks (*Negaprion brevirostris*) within the Atol das Rocan, Brazil. Wetherbee et al. (2007) revealed a high degree of site attachment to lagoon and reef flat tidal pools in young of the year lemon sharks, with larger individuals showing wider ranging and more unpredictable movements encompassing much of the atoll by the end of their first year.

Seasonal migrations are also a well-documented phenomenon for larger species of sharks. Depending on the geographical region, temperature boundaries can shift with changing seasons, which often trigger mass migrations of more mobile species (Musick et al., 2004). Migrations may also be in response to shifts in food sources, or associated with size and sex based segregations within a species (Sulikowski et al., 2016). Such movement patterns have been documented in white sharks (*Carcharodon carcharias*), where tagged individuals migrated between Titi Island, southern New Zealand and the south-eastern coast of Australia (Francis et al., 2015a). White sharks were most abundant at Titi Island during the austral autumn (March–June) which coincided with the peak of adult seal foraging behaviour and pup activity in the area. The greatest number of sharks then left the southern New Zealand location during June, following which they spent approximately six months in tropical to warm temperate inshore and offshore areas off the eastern coast of Australia. With highly mobile species such as the white shark, there is likely a trade-off between the energy expended to travel large distances, and the energy gained from the abundance of food or physiological benefits from being in more optimal environmental conditions. The migratory paths of species can be along continental coastlines, between coastal and oceanic habitats or large-scale transoceanic movements. Therefore, highly mobile species, such as the white sharks described above, can regularly move across multiple jurisdictional boundaries, resulting in the exposure to varying management techniques across their lifetime.

Within the marine environment, connectivity between species and habitats has an important function in determining population dynamics, and nutrient and energy transfer throughout ecosystems by way of predator-prey connections within the food web. Sharks play a significant ecological role in this transfer of energy both within and between systems as juveniles shift from natal grounds, and adult populations connect across habitats, often over large spatial scales and thereby connecting what would otherwise be spatially separated systems. Furthermore, patterns in species dispersal is a crucial factor in determining genetic exchange and resulting diversity. Because sharks either give birth to live young or deposit benthic egg cases, species dispersal is by way of active swimming and is determined by the vagility of the species in question (Musick et al., 2004). However, connections between habitats will also vary depending on the topography and proximity of habitats within a region, with deeper waters having the potential to limit the dispersal of juveniles and wider movements of the adult population (Chin et al., 2013). In such instances where population size is reduced due to a

disconnect from the wider population, genetic isolation and a higher level of inbreeding can occur (Mourier & Planes, 2013).

The daily, seasonal and ontogenetic behaviours of sharks varies between species, as do the specific habitat and feeding requirements. With the added complexities of overlapping ranges of allospecifics and anthropogenic activities, understanding the spatial and temporal structure of populations for conservation management can be a challenging but essential task.

1.4 Sharks as top level predators

1.4.1 Food web dynamics

Food webs are a complexity of ecological connections between producer and consumer species and the corresponding directional transfer of energy between trophic levels in natural communities. It has long been recognised that bottom-up processes via resource control in food webs play an important function in regulating species population size, distributions and the structure of connecting consumer trophic levels in both aquatic and terrestrial systems (Hairston et al., 1960; Rosenzweig & MacArthur, 1963; Oksanen et al., 1981). However, the influence of top-down control through predatory influences attracted debate after it was first acknowledged by Hairston et al. in 1960 (Fretwell, 1987). Hairston et al. (1960) proposed that top-down control, by way of predatory suppression of herbivores, prevented the destruction of basal species. Despite being initially challenged, the importance of predator-prey interactions and the concept of a predator-prey equilibrium garnered support by the 1980's. Oksanen et al. (1981) demonstrated how predators at the higher trophic levels were equally as influential as primary producers, at the lowest trophic levels, in regulating biomass and preventing irruption of consumers along the food web cline. The concept proposed by Oksanen et al. (1981) was then extended by Fretwell (1987), who discussed these complexities and the interchanging nature of food web dynamics. They identified variation over temporal and spatial scales depending on factors such as habitat type, resource availability, fluctuations in resources, intra-species competition, and species vulnerability to predators and defensive ability. Furthermore, a synthesis by Power (1992), identified issues in methodology which along with spatio-temporal co-variables, made it difficult to measure the strength of top-down and bottom-up forces in food webs with confidence. Therefore, it would be prudent to assume top-down forces co-limit communities in

concert with bottom-up forces, rather than being regulated by one variable independently. The strength and importance of each force in the regulation of communities continues to remain one of the fundamental questions in ecology.

1.4.2 Defining an apex predator

When defining top-level predators, species can be divided into apex predator (secondary carnivores) and mesopredator (primary carnivores) subgroupings. The definition of an apex predator varies among the literature, but there are common characteristics presented throughout such as specialised feeding, large-bodied, and a large home range (Heupel et al., 2014). More commonly, apex predators are explained in terms of their trophic position, occupying the highest trophic level in their community (Heupel et al., 2014; Nieblas et al., 2014; Wallach et al., 2015; Roff et al., 2016). A study by Essington et al. (2006) defines apex predators as species with trophic levels greater than 4 (primary producers having a trophic level of 1). They are also considered to have no natural predators (Heupel et al., 2014; Nieblas et al., 2014, Roff et al., 2016). Furthermore, apex predators are attributed to be responsible for the promotion of biodiversity and the structuring of local ecosystems by preventing the monopolisation of limited resources by strongly competing species (Sergio et al., 2006; Wallach et al., 2015). This can be achieved directly through predation, where prey populations are actively maintained at or below the maximum carrying capacity the system's resources can support (Hairston et al., 1960; Rosenzweig & MacArthur, 1963). Indirectly, structure can be created by fear and avoidance of predation influencing the activity level and spatial use of species within the lower trophic levels as they attempt to avoid direct encounters. For example, when influenced by the fear of predation, an individual may avoid foraging areas with a high predation risk (Ripple & Beschta, 2004); forage in different areas in response to predator movements; or reduce overall foraging activity if a predator was present (Schmitz et al., 1997). Such restrictions on habitat use and activity level can have substantial effects on the growth, reproduction and survival of the restrained species (Ritchie & Johnson, 2009). Consumers in the lower trophic levels constantly face a trade-off between optimal energy gain and the risk of predation when foraging, and often forgo food for safety, with the non-lethal effects of intimidation recognised as being just as important as direct mortality itself in regulating species compositions (Brown et al., 1999; Ritchie & Johnson, 2009). Direct predation and anti-predator responses restrict population size, prevent the overexploitation of resources,

reduces localised impacts, and allow a diversity of species to utilise a habitat. Where predatory influences are missing, or have been removed, reductions in species densities (Sergio et al., 2006) and the occurrence of trophically simpler food web systems (Paine, 1966) have been demonstrated. The direct and indirect effects of top predatory influences cascading down through the food web and their contribution towards controlling community structure and biodiversity, has led to many apex predator species being considered keystone species – a species whose effects on the system are inordinate in comparison to their abundance within associated ecosystems (O'Gorman & Emmerson, 2009).

In contrast, smaller sized mesopredators can be defined as mid-ranking predators (Prugh et al., 2009), also occupying a high predatory trophic level, but are at a lower trophic tier than, and are predated on by, apex species (Roff et al., 2016). Mesopredators have smaller home ranges, often showing a level of fidelity to associated habitats (Roff et al., 2016) and because they are more generalist hunters, have the ability to impact a wide range of prey species (Ritchie & Johnson, 2009). Predation of mesopredator species by apex species can have large structural effects on mesopredator populations (Ritchie & Johnson, 2009), and contains the total predation pressure. This prevents mesopredator release (Wallach et al., 2015), whereby the population density and distribution of mid-sized predators increases due to a reduction or removal of predation pressures from apex species (Prugh et al., 2009), resulting in an increase in predation intensity on smaller prey species (Ritchie & Johnson, 2009). Therefore, smaller prey species may indirectly benefit from the presence of the apex tier.

However, the ambiguity of these terms has led to a difficulty in defining a line where mesopredators end and apex predators begin. This is further confounded by the complexity of food webs and the occurrence of predatory behaviour over multiple trophic levels, such as omnivory as well as overlapping resource utilisation (Oksanen et al., 1981). A study by Wallach et al. (2015) argued that because large predators tend to be relatively free from predation themselves, and studies on their population regulation by means of bottom-up forces is contradictory, that populations of apex predators are controlled by a self-regulated socially mediated force. They proposed that where species are no longer regulated by predation pressures, that this marks the transition between meso- and apex-predatory roles, and successfully demonstrated such a transition in 12 carnivore families with reproductive strategy being the main contributor to population

control. Wallach et al. (2015) further argues that apex and mesopredator species are also fixed, i.e. if an apex species is removed from a habitat, a mesopredator species cannot become an apex predator, and perform the ecological function of the now absent apex group. This is likely due to morphological adaptations which restrict such a shift in trophic level position. Species that are larger in body size tend to require larger prey items to meet dietary needs (Carbone et al., 2007; Heupel et al., 2014). Features such as body size and gape size, may restrict a mesopredator's ability to predate upon the same and potentially larger prey sources of the original apex species. The greater energetic costs experienced by hunting larger prey items (Carbone et al., 2007) may also make the predation of these species energetically taxing rather than beneficial for the mesopredator tier. Morphology may also prevent mesopredators from being able to utilise similar sized home ranges or enforce the same behavioural effects on communities as apex species, restricting their ability to entirely fulfil the top-down pressures on lower trophic levels usually experienced from the presence of the apex group.

Furthermore, mesopredators have adapted to population regulation influenced by the predation by apex species. When released from predatory forces, their ability to successfully compete for a shared resource (due to a more generalised diet) (Prugh et al., 2009), along with a higher reproductive rate than their apex counterparts (Wallach et al., 2015), can result in population irruptions in the mesopredator tier, altering ecosystem structure from what was maintained by the apex species. When defining apex and mesopredator species, it is also important to note that communities are structured by size rather than species due to the occurrence of ontogenetic diet shifts as individuals grow (Heupel et al., 2014). Because food choice is often determined by size, large-bodied species that are considered to be 'apex' may display a level of prey overlap with mesopredator species in earlier stages of ontogeny before larger prey items are consumed as an adult. The clarification of species into 'apex' or 'mesopredator' groupings, along with the understanding of the direct and indirect top-down forces they place on species within their associated communities, is integral if ecologists are to elucidate the role various top predator species play in the regulation of community size and structure, and overall sustainability of ecosystems.

1.4.3 Trophic cascades

The role top predators play in various ecosystems continues to be of importance to ecologists and conservationists as large carnivorous species continue to be removed from habitats (Ripple & Beschta, 2004) through exploitation, persecution, and habitat loss and fragmentation (Ritchie & Johnson, 2009). In addition to understanding predator-prey dynamics, an equally important question is – what are the ecological consequences following the removal of top predators from natural communities? The continuation of the direct and indirect effects of top-level predators through successively lower trophic levels down to the basal tier can be defined as a top-down trophic cascade (Ripple & Beschta, 2004), and can signal the presence and strength of top-down predatory forces within communities (Schmitz et al., 1997). Disruptions to this cascade of interactions by way of species removal can have substantial effects on ecosystems, such as altering energy flow, community composition (particularly at the autotroph level) and habitat allocation, along with secondary extinctions (O'Gorman & Emmerson, 2009). Food webs are constantly mobile, responding to spatio-temporal changes such as environmental variation, nutrient cycling, predator-prey dynamics and behaviour, intra- and inter-species competition, life histories and habitat disturbances. The effects of such co-variables make it clear that the influences of predatory and resource control are not the only pressures regulating communities. However, despite such ecosystem complexity, experimental studies have demonstrated quantifiable responses of communities to perturbations at the higher trophic levels and the vulnerability of basal species to such events.

A well described example of the effects of direct predatory forces on the trophic cascade is that reported by Estes et al. (1978), who demonstrated the influence of sea otter (*Enhydra lutris*) predation on an important prey species, the sea urchin (*Strongylocentrotus polyacanthus*), along with the indirect trophic effects on macroalgal associations in nearshore communities. After historically being exploited to near extinction by fur traders, sea otter populations recovered over a limited extent of their original range, and where present, have been reported to limit the size and density of sea urchin populations well below that which can have a destructive impact on macroalgal assemblages, resulting in high levels of primary production in nearshore communities (Estes et al., 1978). A greater diversity of species within the nearshore community was also noted in areas where sea otters had recovered. In contrast, in areas where sea otters were absent, sea urchins were shown to be more abundant, larger in size and eliminated

macroalgal cover through overgrazing (Estes et al., 1978). Further study demonstrated that such top-down forces remained apparent when other co-variables such as natural variation, habitat type, echinoid recruitment and selective foraging by the sea otters were considered (Estes & Duggins, 1995).

Behaviourally mediated trophic cascades have also been documented within the literature. A long-term study by Heithaus et al. (2007a) investigated the importance of the non-consumptive influences tiger sharks (*Galeocerdo cuvier*) had on seagrass communities within Shark Bay, Western Australia. Within the bay, green sea turtles (*Chelonia mydas*) had a year round presence as they grazed on offshore, subtidal sea grass meadows. The primary species of sea grass in the bay was *Amphibolis antarctica*, which due to the distribution of important organic carbon and nitrogen chemical components, was of better quality in the shallower interior microhabitats of sea grass banks, with poorer quality sea grass growing on the outer bank edges nearer the deeper channels. Because sea turtles use tactics such as bursts of speed and sudden changes of direction to evade predators, the shallower, interior areas of higher quality sea grass also posed a greater risk due to a lack of escape routes and a greater distance to the deeper channels where there was a greater probability of predatory sharks being outmanoeuvred. Because their only predator, the tiger shark, showed seasonal variation in abundance, being present only during the summer months, this allowed researches to assess the importance of predation risk in the feeding behaviours of these basal consumers (Heithaus et al., 2007a).

When tiger sharks were absent from Shark Bay, foraging location of turtles was spread across sea grass habitat proportional to the quality of the food supply. However, as predation risk increased through the presence of tiger sharks, turtles shifted from the shallower, interior bank areas where sea grass quality was highest to the deeper, outer bank edges. Although encounters with tiger sharks were more probable along the bank edges, the deeper water was paired with a greater likelihood of escape. Similar behaviours have also been noted in dugongs (*Dugong dugon*) and bottlenose dolphins (*Tursiops aduncus*) (Heithaus et al., 2012), demonstrating the role behavioural influences can have on prey assemblages in limiting patterns and intensity of resource exploration across space and time, and allowing the persistence of valuable resources across a habitat. Moreover, this research further reinforced how populations of foraging

species are not solely influenced by bottom-up processes, with resource availability also being a function of predation risk.

It is now widely accepted throughout the literature that top-level predators promote the diversity of natural systems by suppressing population irruptions and driving basal productivity (Paine, 1966; Estes et al., 1978; Berger et al., 2001; Shurin et al., 2002; Ripple & Beschta, 2004; Ritchie & Johnson, 2009; Wallach et al., 2015). Moreover, there is further evidence to suggest that greater biodiversity within communities (and thus a diversity of responses by species to variable conditions, see Sole & Montoya, 2001) dampens the effects of any perturbations within the trophic cascade, with the interaction strength of a single species diffusing among multiple pathways of the food web (Schmitz et al., 2000). Strong (1992) argued that the effects of disruptions to trophic cascades are restricted to systems of low diversity where the interactions of only one or a few species (analogous to a keystone species) have great influence over community function, and when the basal community is composed entirely of species that are edible to the herbivore tier, unifying consumption. More complex and diverse food webs can also be characterised by a small number of these strong interactions, but are also surrounded by a number of weak interactions (O'Gorman & Emmerson, 2009). O'Gorman & Emmerson (2009) demonstrated that ecosystem complexity was not enough to fully protect against the cascading effects following the removal of strongly interacting species. However, the weak interactors within the system played a vital, community wide role, buffering the destabilising influences of the strong interactors, where functionally capable species replace extinct ones (Sole & Montoya, 2001), allowing the community to persist. Less diverse systems do not have this redundancy. When weak interactors were removed by O'Gorman & Emmerson (2009), variability within the primary and secondary trophic tiers increased, identifying the importance of the function of both strongly interacting species and those beyond the keystone nodes of the food web in sustaining population, community and ecosystem dynamics of natural communities and their ability to withstand change. Strong (1992) also argued that in diverse systems, spatio-temporal variation among trophically similar species along with the occurrence of interactions such as omnivory and generalist feeding, also provided a buffer against intensive consumption assisting in the prevention of a trophic trickle from becoming runaway consumption. It is suggested that runaway consumption in speciose systems is due to perturbations imposed by man that are too severe to be buffered by natural processes (Strong, 1992). This is supported by a model by Sole & Montoya

(2001) who found significantly higher levels of extinction rates following selective attacks on highly connected nodes of the food web, synonymous to keystone species, and highlighting the importance of the identification of highly connective species in protective management.

The 'Green World Hypothesis' of Hairston et al. (1960), suggested that food webs interacted in a linear fashion with distinct trophic levels, and are usually the architecture found in trophic cascades (Strong, 1992). However, Polis et al. (2000) argued that it was unrealistic to compartmentalise species into discrete chain-like trophic levels due to the more web-like manner in which interactions behave. It is also important to acknowledge that due to the strength and ability of interactions to effect the wider community varying, not all trophic interactions cascade (Strong, 1992). This brings to attention the need to distinguish the difference between a species level trophic cascade, which occur in only a compartment of the food web and effect only one or a few basal species, and a community wide trophic cascade, which can substantially alter the composition and distribution of basal species throughout the entire system (Polis, 1999). The loss and fragmentation of basal production to this extent can have great influence over community composition by way of bottom-up resource control, along with reducing the number of available refuges that assist in the avoidance of direct interspecies encounters (Ritchie & Johnson, 2009). Thus, species level cascades do not hold the same significance as community level cascades when considering system wide changes in the structure and function of an ecosystem (Polis et al, 2000).

Despite the documentation of examples of trophic cascades throughout the literature, it is clear that debate remains over the presence of top-down predatory control, and the role it plays in maintaining community structure and function. For example, a discussion by Roff et al. (2016) raises one such debate which argued that the presence of a shark (top predator) driven trophic cascade was weak with shark species providing little benefit to the coral reef community. However, one could argue that this weak predatory influence is a result of the complexity and high functional redundancy found within coral reef communities, dampening effects and preventing detection. Furthermore, the work of Ruppert et al. (2016) refuted the conclusions drawn by Roff et al. (2016), and strongly supported the presence of top-down influences of sharks on species abundances down to the basal tier. Ruppert et al. (2016) further identified issues in methodology of Roff et al. (2016) and similar studies, which failed to

acknowledge that species abundances were influenced by both top-down and bottom-up processes, and only monitored change over limited temporal and spatial scales. As Hairston & Hairston (1997) state "any attempt to understand broad ecological patterns will be challenged by the complexity of nature," with inconsistencies in scientific method leaving room for conflicting evidence between ecological theorists.

Natural communities are largely heterogeneous through space and time. As a result, food web structure and function is never constant (Polis, 1999), and along with a scarcity of high quality data and methodological limitations (Sole & Montoya, 2001), adds to the difficulty in identifying trophic cascades and the way they influence varying natural communities. This contextual nature of food webs means we may be limited in our ability to make universal theoretical assumptions on food web dynamics, but instead recognise patterns in, and consequences of, certain disruptions to certain types of systems. There is evidence that complex systems come with ecosystem stability. However, the strength of predatory effects and the role of predation in ecosystem structure and function can be unclear in complex systems due to species diversity and higher levels of redundancy compensating for any trophic disruptions (Roff et al., 2016). Furthermore, because basal resources can be influenced with process at the top of a food web, bottom-up processes must be considered simultaneously with top-down forces if ecologists are to understand the strength of patterns of control and the role it plays in community organisation (Ritchie & Johnson, 2009). There is still much room to improve our understanding of such food web dynamics, not only the strength and structure of inter- and intra-guild and multitier interactions, but also across taxonomic groups and ecosystems if we are to unequivocally understand the consequences of top predator removal to associated communities (Prugh et al., 2009).

1.4.4 Loss of sharks from marine ecosystems

As trophic level increases, species richness decreases in comparison to basal species (Duffy, 2003). Thus, top predatory species are more susceptible to local extinctions than those lower in the food web cline (Oksanen et al., 1981; Petchey et al., 1999; Duffy, 2003). Despite their vulnerability, large apex consumers continue to be removed from the environment. Valued for their fins, meat, skin and liver oil, the industrialisation of fisheries remains the greatest threat to shark populations, accounting for 96.1% of reported mortalities globally and substantial population declines and diversity loss

worldwide (Ferretti et al., 2010). Initially, sharks were considered low value by-catch of more profitable billfish and tuna fisheries (Davidson et al., 2016), and thus deemed low priority within fisheries management processes (Barker & Schluessel, 2005). As a result, detailed catch and survey data for population assessments are limited with changes in many populations remaining undocumented until recently (Ferretti et al., 2010). However, the past few decades have seen rapid expansion in the exploitation of sharks, with reductions in other valuable fisheries stocks (Davidson et al., 2016), and technological, processing and marketing advances boosting shark products as a more valuable fisheries resource (Barker & Schluessel, 2005). Furthermore, new finning regulations requiring the entire body to be landed, not just the fins, has developed a market and therefore greater demand for their meat (Dent & Clarke, 2015). In 2011 (the last year for which global data was available), global revenue from the trade of shark products was in excess of USD800 million (Dent & Clarke, 2015). Of this, USD379.8 million was accounted for by meat exports and was a 42% increase from the previous decade (Dent & Clarke, 2015). However, despite their expansion, shark fisheries still constitute a small proportion of the wider fishery for many countries (Barker & Schluessel, 2005), and as such, the overall cost of assessing each stock often costs more than the overall revenue of the fishery (Ferretti et al., 2020). As a result, large proportions of shark fisheries remain either overfished or unassessed (Ferretti et al., 2020), with an overall global reduction in fisheries landings being attributed to population declines, rather than the improvement of fisheries management controls (Davidson et al., 2016).

Furthermore, the geographic expansion of fisheries and the associated increase in fisheries effort and catch has been shown to coincide with a decline in the mean trophic level of fish species caught (Pauly & Palomares, 2005) – a process that can be referred to as trophic downgrading (Estes et al., 2011). Trophic position is a measure that positively correlates with body size (Jennings et al., 2002). It is now unanimous throughout the literature that the mean trophic level of fisheries catch is declining, resulting in the addition of new fisheries and the simultaneous exploitation of multiple trophic levels, as a reduction in larger species leads to smaller species also becoming targeted (Essington et al., 2006). Both ecosystem models and *in situ* evidence support the cascading effects that result in the loss of sharks and other large predatory species from marine communities (Ferretti et al., 2010). For example, in the northwest Atlantic, there was an overall decreasing trend in the average fork length of shark species

providing consistent estimates in population declines, which was accompanied by a general pattern of increasing abundance of smaller mesopredator species (Myers et al., 2007). Similarly, an analysis of observer data from longline fishing vessels working in the tropical pacific identified an average decline of 21% of the most abundant large pelagic predator species – sharks, billfishes and large tunas. As in the previous example, this coincided with an increase in abundance of smaller mesoconsumer species such as the great barracuda (*Sphyraena jello*) and the formerly rare pelagic stingray (*Dasyatis violacea*) (Ward & Myers, 2005).

The life history characteristics of sharks (slow growth, late maturity, low fecundity, long gestation) limit a population's ability to recover under continued extractive pressure. Such traits can also mean the effects of population declines on the wider ecosystem regime can display substantial time lags (Dulvy et al., 2004; Davidson et al., 2016), making trophic cascades difficult to identify and understand. Furthermore, such cascades can result in the decline of other commercially valuable species as a consequent of mesopredator release and increased predation pressure in the lower levels of the food web. Such an impact was demonstrated along the Kwala-Zulu Natal shore in South Africa. A 50 year shark netting program alongside recreational fishing tournaments reported declines in the catch per unit effort (CPUE) of large sharks which coincided with a proliferation of smaller elasmobranchs and declining populations of recreationally important bony fish species (van der Elst, 1979). It is evident that the ecological role of large predatory sharks is met by their importance to the wider fisheries that they sustain. However, shark fisheries will continue to trade to meet an insatiable market. Therefore, it is imperative that research into the ecology and biology of such populations is supported to enable effective guidance of regional and global management strategies.

1.5 Sharks in New Zealand

1.5.1 An overview

New Zealand's archipelago, comprised of two major islands and over 700 offshore islands and islets, spans 2600 km and over 24° of latitude of the Pacific Ocean (Gordon et al., 2010; Francis, 2012). Two major water masses influence New Zealand's marine environments. Sub-tropical waters span from the Kermadec Islands at the most northern point of New Zealand down to the Snares Islands in the south, with sub-

Antarctic waters extending south of the Snares Islands (Francis, 1996). These water masses are separated by the subtropical front which position varies depending on the season (Francis, 2012). These different water masses result in a broad range of temperatures across New Zealand waters, from around 24°C at the Kermadec Islands, to around 9°C at Campbell Island at the most southern point of New Zealand's range (Francis, 2012). The extent of the range of New Zealand landmasses results in a diversity of temperature influenced habitats, which in turn effects the distribution of species and diversity within communities present in these waters.

New Zealand has the fourth largest Exclusive Economic Zone (EEZ) in the world (Francis, 1998), spanning over 4 million km² with species within this zone representing approximately 8% of global marine species (Gordon et al., 2010). Of this, there are 73 known species of sharks (Ministry of Fisheries, 2008), which utilise a range of habitats from shallow estuarine, harbour and coastal areas, to the outer shelf, pelagic and deep-sea environments. While seven of these species are protected or restricted from being targeted by fishing activities (Table 1.1), others hold significant commercial value or are targeted in customary, recreational and large game fisheries. However, commercial fisheries remain responsible for the majority of shark catches (Francis, 1998). Including skates, rays and chimaeras, a reported 90% of all catch is comprised of species managed under the Quota Management System (QMS) (Ministry for Primary Industries & Department of Conservation, 2013), encompassing six species of shark (Table 1.1). Included in this are highly migratory species such as the mako (*Isurus oxyrinchus*) and blue shark (*Prionace glauca*) which can have large home ranges and have been shown to move across multiple jurisdictional boundaries during different times of the year (Nakano & Stevens, 2008; Francis et al., 2019), exposing them to varying management techniques. The remainder of species are exposed to unmanaged, open access fishing.

Table 1.1: Management categories of sharks in the New Zealand fisheries management system (adapted from Ministry for Primary Industries & Department of Conservation, 2013).

Protected (species for which utilisation is not considered appropriate)	**Schedule 4C of the Fisheries Act 1996** (may not be targeted)	**Quota Management System** (90% of all catch)	**Open Access** (species that are not protected, included in QMS or on Schedule 4C
Sharks: Basking Shark (*Cetorhinus maximus*) Whale shark (*Rhincodon typus*) Oceanic whitetip shark (*Carcharhinus longimanus*) White shark (*Carcharodon carcharias*) Deepwater nurse shark (*Odontapsis ferox*) **Skates and Rays:** Manta Ray (*Manta birostris*) Spinetail devil ray (*Mobula japanica*)	**Sharks :** Hammerhead shark (*Sphyrna zygaena*) Sharpnose sevengill shark (*Heptranchias perlo*)	**Sharks:** Spiny dogfish (*Squalus acanthias*) School Shark (*Galeorhinus galeus*) Rig shark (*Mustelus lenticulatus*) Mako Shark (*Isurus oxyrinchus*) Porbeagle shark (*Lamna nasus*) Blue shark (*Prionace glauca*) **Skates and Rays:** Smooth skate (*Dipturus innominatus*) Rough skate (*Zearaja nasutus*) **Chimaeras:** Dark ghost shark (*Hydrolagus novaezelandiae*) Pale ghost shark (*Hydrolagus bemisi*) Elephantfish (*Callorhinchus milii*)	All other species not listed elsewhere in this table

1.5.2 Sharks in the Bay of Plenty

The Bay of Plenty is on the east coast of the North Island of New Zealand. The area has a primarily warm temperate climate, with sub-tropical waters influencing the region during particularly warm summers. The Bay of Plenty hosts a diversity of habitats such as sandy and rocky coastlines, estuaries and marshlands, sheltered bays, exposed headlands and offshore reefs and islands. Within the region are two marine protected

areas, Tuhua (Mayor Island) Marine Reserve and Te Paepae o Aotea (Volkner Rocks) Marine Reserve, providing complete protection from fishing and other extractive activities, dumping, construction and any other direct human disturbance within their boundaries. In addition, a new protected area under an alternate coastal management plan was announced in February 2021 for reef and islet areas surrounding Motiti Island. These protected and unprotected habitats support a diversity of shark species throughout the year, from coastal species such as bronze whaler (*Carcharhinus brachyurus*), smooth hammerhead (*Sphyrna zygaena)* broadnose sevengill (*Notorynchus cepedianus*), school (*Galeorhinus galeus*) and rig (*Mustelus lenticulatus*) sharks, to more wide-ranging pelagic species such as mako, blue, and white sharks. Deep-water species such as the bluntnose sixgill (*Hexanchus griseus*) have also been reported, as well as tropical species such as tiger (*Galeocerdo cuvier*) and whale sharks (*Rhincodon typus*) during the summer months when sub-tropical waters influence the region.

Despite a diversity of species, our knowledge of shark populations in the area is limited to a catch per unit effort analysis of school sharks (Starr & Kendrick, 2010); estimations of bycatch from tuna longline fisheries which reported blue, mako, porbeagle, (*Lamna nasus*), school shark and dogfish (Family Squalidae) species (Francis et al., 1999; Francis et al., 2001); and a survey investigating rig shark nursery grounds within the Tauranga Harbour (Francis et al., 2012). All other information is based on reports from local recreational fishermen, game catch reports and further commercial data. However, information from commercial fisheries is restricted by biases such as gear selectivity targeting certain species or life stages, fishing effort being in locations where species are most likely to be encountered and data limitations (White et al., 2013; Sherman et al., 2018). As a consequence, the full extent of species distributions, particularly for wider ranging species, is not recognised (White et al., 2013).

In addition to our limited understanding of the life histories of species in the area, sharks that frequent the region are susceptible to a number of anthropogenic effects. Human settlements boarder the coastline and estuarine systems, polluting adjacent waters through surface run-off and sewage outfall discharges, with nutrient input from surrounding catchments transported by a number of tributaries discharging into various estuarine and coastal habitats. The region also hosts the largest commercial shipping port in New Zealand, with regular dredging of harbour channels required to maintain shipping and boating lanes, along with occasional oil and fuel spills within the direct

shipping facility. The ballast waters of ships and movement of other commercial and recreational vessels into the area also present a biosecurity threat through the transportation of foreign organisms, threatening native flora and fauna. Commercial fisheries are attracted to nearshore and offshore areas of the region by the rich diversity of habitats and the species they host. However, the indiscriminate nature of many fisheries threatens the populations of both target and non-target species. The accessibility of habitats within the region also place species under additional pressure from a popular boat and land-based recreational and game fishery. Indeed the area is not exempt from global issues such as micro- and macro-plastic pollution, nor the effects of climate change. As it is, shallow nearshore waters already possess varying physical characteristics both on a temporal and spatial scale which inhabiting species must tolerate. Inner harbour and estuarine environments in particular experience major fluctuations in salinity, temperature, depth, flow and turbidity due to changes in tidal level, freshwater inflow and rainfall (Knip et al., 2010), with outer harbour areas being more susceptible to seasonal weather patterns and storm events.

1.6 Bronze Whaler Sharks (*Carcharhinus brachyurus*)

The bronze whaler shark (*Carcharhinus brachyurus*) is a member of the Carcharhinidae family (also known as requiem sharks). The genus *Carcharhinus* radiated during the Middle Eocene (45mya), and is the most speciose of the 12 genera that make up the Carcharhinidae group (Musick et al., 2004). Its 31 members have a primarily tropical / sub-tropical distribution, with the exception of *C. brachyurus*, which is the only member of this genus that associates with warm temperate environments (Walter & Ebert, 1991). Bronze whaler sharks have a circa-global distribution, although it is patchy, and presently this species is absent from the western North Atlantic despite being abundant in this area during the Miocene (Musick et al., 2004). Considered a coastal species (Garrick, 1982; Cliff & Dudley, 1992; Da Silva & Bürgener, 2007; Benavides et al., 2011; Drew et al., 2016), the bronze whaler shark can be found utilising inshore areas such as harbour and estuarine environments, sandy and rocky coastlines, and nearshore islands. However, its range also extends further offshore into neritic shelf habitats where it has been recorded down to a depth of 100 m (Smale, 1991; Cliff & Dudly, 1992; DaSilva & Bürgener, 2007; Bradshaw et al., 2018).

This species is known to travel long distances, with tag and release studies reporting movements by individuals up to 2315 km (Cliff & Dudley, 1992; Rogers et al., 2013). Such wide-ranging movements were further supported in a study by Benavides et al. (2011) which failed to detect differences in genetic structure between 2700 km of coastline between South Africa and Namibia. However, movement typically remains shelf-associated with transoceanic movements yet to be documented. Circa-globally, there are consistencies in morphological features such as body proportions, fin shape and teeth (Garrick, 1982). However, the number of precaudal vertebrae can vary with the greatest differences being between populations on either side of the Atlantic, indicating the role of this transoceanic barrier in gene transfer between geographically different populations (Garrick, 1982). This observation is further supported by Benavides et al. (2011), who demonstrated that bronze whaler populations in the southern hemisphere were not panmictic, with isolated vicariant populations being separated by deep oceanic expanses.

Patterns in recreational and commercial catches also indicate a seasonal influence on the movement patterns of bronze whaler sharks. Reports on populations in Australia (Drew et al., 2019), New Zealand (Cox & Francis, 1997), South Africa (Smale, 1991), and Argentina (Lucifora et al., 2005) indicate this species is absent from coastal environments during the austral winter with numbers then peaking during the summer months. Seasonal movements have been linked to changes in water temperature (Lucifora et al., 2005), feeding behaviour (Cliff & Dudley, 1992) and the use of coastal areas for parturition and mating (Izzo et al., 2016). For example, using acoustic telemetry, Drew et al. (2019) reported a strong seasonal pattern with increasing acoustic detections from tagged bronze whaler sharks within the Gulf St. Vincent during the summer period (September to April), which coincided with increases in ambient water temperatures. Furthermore, the majority (77%) of tagged sharks returned to the gulf for up to four years (the duration of the study) indicating site fidelity is a strong factor in these seasonal movements. During the winter (May to August), presence and time spent within the gulf then declined along with the decreasing water temperatures during these months. The analysis of vertebral chemistry on populations in South Australia has also revealed a strong spatial component in vertebral edge data indicating seasonal influences on population structure (Izzo et al., 2016). In most cases, the wintering grounds remain unknown.

Named for the copper-bronze colour of their dorsal surface, this species lacks an inter-dorsal ridge (Garrick, 1982), which is the most easily distinguishable feature when separating it from the dusky shark (*Carcharhinus obscurus*) with which it is often confused (Cliff & Dudley, 1992). Sexual dimorphism is present in this species, with females growing larger than males to a maximum total length (TL) of 308 cm (Drew et al., 2016) and 294 cm (Walter & Ebert, 1991) respectively. Males reach sexual maturity between 200–220 cm TL, aged 13–17 years, while females have been found to mature within a wider range between 215–271 cm TL and aged 16–20 years (Garrick, 1982; Smale, 1991; Walter & Ebert, 1991; Lucifora et al., 2005; Drew et al., 2016). The highest recorded age in this species is 30 years in males (Walter & Ebert, 1991) and 31 years in females (Drew et al., 2016). This species can be found alone, or grouped in pairs or single sex schools of similar size (Smale, 1991; Cliff & Dudley, 1992). Gestation is estimated to last 1 year (Smale, 1991; Cliff & Dudley, 1992) with parturition thought to occur biennially from October to December (Walter & Ebert, 1991; Cliff & Dudley, 1992; Lucifora et al., 2005). Reproductive mode is viviparous where pups maintain a placental link within the mother's uterus until born as fully developed free-swimming individuals (Smale, 1991; Rogers & Huveneers, 2009). Litter size ranges from 8–26 pups (Cliff & Dudley, 1992; Drew et al., 2016), with embryos growing up to 67 cm TL (Garrick, 1982; Drew et al., 2016) and new born sharks ranging in length from 58.5–83.5 cm TL (Garrick, 1982; Smale, 1991; Walter & Ebert, 1991). Litters typically have a male to female sex ratio of or close to 1:1 (Smale, 1991; Drew et al., 2016). Bronze whaler sharks are the slowest growing member of the genus *Carcharhinus*, attributed to the colder climate in which they are found (Walter & Ebert, 1991). Paired with a high age at maturity and low fecundity, this contributes to the vulnerability of this species to overexploitation and other contributing anthropogenic threats, hence its classification as near-threatened by the IUCN (Duffy & Gordon, 2003).

In New Zealand, the bronze whaler shark is prohibited from being commercially targeted in coastal fisheries. However, this species is still taken as a bycatch species with landings increasing since 1992–93 (Francis, 1998). Biochemical identification techniques have also confirmed the landing of this species for fin and meat markets mislabelled as commercially managed species such as the rig shark (Smith & Benson, 2001). Furthermore, it is caught in a popular recreational game fishery, particularly from shore based anglers during the summer months (December–April), but now

primarily under a catch-and-release system after an upsurge in the popularity of this method since the late 1980's, resulting in a reduction in sharks landed (Francis, 1998; pers. obs.). Overseas, the bronze whaler is a valuable commercially targeted species. Although not typically consumed in South Africa, the bronze whaler shark is an important species in their unrestricted demersal shark fishery. Despite limited knowledge of stock status and the impacts of current harvest levels, their high value meat continues to be exported to meet the needs of the Australian market – primarily in the fish and chip trade (DaSilva & Bürgener, 2007). In Australia, bronze whaler sharks are caught throughout their range, particularly in South Australia where there is a seasonal target commercial fishery for this species (Drew et al., 2019). Coinciding with their seasonal movements, sharks in the pelagic fishery from shelf and gulf habitats in Australia showed the highest number of catches occurring between November to March (austral summer) with only 10% being caught during winter (Rogers et al., 2013). Smaller target fisheries are active in Namibia, Argentina, Mediterranean, Uruguay and Brazil (Bradshaw et al., 2018). As in New Zealand, the bronze whaler shark is also caught by social and competitive anglers in South Africa (Pradervand & Govender, 2003), Australia (Bradshaw et al., 2018), Argentina (Lucifora et al., 2005), and the Mediterranean (Duffy & Gordon, 2003).

Bronze whaler sharks have a broad niche width indicating the species incorporates a diverse diet (Rogers et al., 2012). Pelagic teleosts make up the most dominant prey groups of bronze whaler sharks in studies in Argentina (Lucifora et al., 2009), South Africa (Cliff & Dudley, 1992) and Australia (Rogers et al., 2012). These species are typically small (<35 cm) in length (Smale, 1991; Cliff & Dudley, 1992). Less important components include demersal teleosts (Lucifora et al., 2009) and invertebrates such as cephalopods (Cliff & Dudley, 1992; Lucifora et al., 2009). However, benthic teleosts and benthic cephalopods have been shown to also be important in the diets of bronze whaler sharks in southern Australia (Rogers et al., 2012), indicating possible geographical variation in diet composition. Alternatively, this may be a reflection of the size range of sharks caught in these studies, with the south Australian study testing a greater range (71–305 cm TL) compared to 100–256 cm TL and 102–237 cm TL in Argentina and South Africa respectively. The predominance of smaller individuals potentially still utilising shallower nursery habitats could explain the greater reliance on these benthic prey groups. Squid were also dominant components in the diets of bronze whaler sharks in a separate study in South Africa by Smale (1991). But again, this may

have resulted from the lengths of sampled sharks, which were primarily <200 cm TL in this study. Pelagic pilchards are an important food source seasonally for this species in South Africa, with the migration of pilchards along the coastline and shelf coinciding with high numbers of bronze whaler sharks among other species such as birds, fish and marine mammals. The annual interactions between these species indicates that prey distribution is an important factor in determining the movements of bronze whaler sharks. Bronze whaler sharks have also been reported scavenging on the carcasses of marine mammals such as dolphins and whales (Cliff & Dudley, 1992), as well as live catch and frame discards from fishermen (Rogers & Huveneers, 2009; pers. obs.).

A consistent observation is that diet expansion is evident in this species with larger prey items being incorporated into the diet with growth (Lucifora et al., 2009). This includes the consumption of elasmobranchs, mostly small sharks in individuals >200 cm TL (Smale, 1991; Lucifora et al., 2009). However, small prey items still remain an important dietary component (Smale, 1991; Lucifora et al., 2009), possibly due to the low cost of capture and high encounter probability of this prey (Lucifora et al., 2009). With diet expansion comes trophic niche expansion indicating the importance of larger individuals to ecosystem stability as their wider trophic niches influence more trophic links than smaller, trophically-restricted individuals.

Within the literature, the bronze whaler shark is referred to as an apex predator (Benavides et al., 2011). Furthermore, this species meets the criteria outlined by Roff et al. (2016) which defines apex predatory sharks as growing in excess of 3 m total length, utilising large home ranges across multiple habitats, and having a limited threat of natural predation. However to date, no studies in New Zealand have directly assessed the trophic ecology of the bronze whaler shark to confirm these assumptions. Similarly, there is no published data on population or movement data available for this region.

1.7 Research statement and objectives

Despite their declining abundance, sharks are considered to be among the most diverse predators within marine ecosystems (Roff et al., 2016). Due to the wide-ranging movement behaviour of many shark species, their role as top-level predators can influence the structure and function of communities across multiple habitats. Therefore, in order to understand the predatory effects large sharks have on an ecosystem, an

understanding of their spatiotemporal movement patterns is required. Although research has begun to elucidate the biology and ecology of the bronze whaler shark, this species remains largely understudied despite being considered common in coastal waters. Summer movements are predictable with frequent sightings within coastal environments from November to April each season. However, during the remainder of the year sightings and interactions with fishermen cease, with the thought that this species shifts into offshore waters during these winter months. Albeit, it remains unknown if they continue to gain sustenance from coastally-derived food webs, or if they shift to a pelagic-based food web system. Perhaps it is a combination of the two? Thus, the overarching goal of this research is to investigate the habitat use and trophic ecology of bronze whaler sharks to establish their role as top-level predators within coastal Bay of Plenty waters. Furthermore, this research aims to build on current knowledge to ensure sound management decisions regarding this species, and to understand the possible cascading effects on associated ecosystems if they are removed through either natural or anthropogenic processes.

Specific objectives include:

- To test the efficacy of satellite-linked smart position or temperature transmitting (SPOT5) tags in providing spatiotemporal data on bronze whaler sharks for which surfacing behaviour is unknown

- To obtain preliminary insights into the long-term movement patterns of bronze whaler sharks in New Zealand at a spatial scale of up to tens of kilometres, and over time periods of days to months

- To identify if temperature is an environmental factor influencing the seasonal movement patterns of this species

- Using $\delta^{13}C$ and $\delta^{15}N$ stable isotopes, investigate the position of bronze whaler sharks relative to the wider coastal community within the Bay of Plenty

- Investigate $\delta^{13}C$ and $\delta^{15}N$ stable isotopes as indicators of the most important prey items of bronze whaler sharks

1.8 Organisation of the thesis

This thesis is organised into four chapters including the introduction and general discussion sections. Chapter 1 provides an overview of sharks and their importance as top-level predators within marine communities. In addition, details on current knowledge of the biology and ecology of bronze whaler sharks are described. Chapter 2 investigates the use of satellite-linked tags in determining the spatiotemporal distribution of bronze whaler sharks, and provides a preliminary assessment of their movements as they transition from the summer coastal region into unknown wintering habitats. Chapter 3 then uses stable isotope analysis to further investigate habitat use through food web interactions, along with dietary contributions of prey species and trophic position estimates to provide insight into the role bronze whaler sharks play as top-level predators within the coastal marine environment. Chapter 4 discusses the final findings of the multidisciplinary approach used by this research, and synthesises observations and data from throughout the thesis in the context of the literature.

Chapter 2

Movement patterns of adult female bronze whaler sharks (*Carcharhinus brachyurus*) in north-eastern New Zealand revealed using satellite-linked smart position or temperature transmitting (SPOT5) tags

2.1 Introduction

Large marine apex predators such as sharks play a disproportionately important role in regulating the structure and function of associated ecosystems through their direct and indirect influence on species composition, biomass, trophic roles and behaviour of prey assemblages (Ferreira et al., 2015; Heupel et al., 2015). Furthermore, those species that move between different communities link spatially separate food webs, thus transferring energy between and influencing multiple systems across vast spatial scales (Abrantes & Barnett, 2011; Heupel et al., 2015). As a result, their depletion through extractive anthropogenic activities can have cascading effects throughout the food web leading to ecosystem shifts and altered resilience in both coastal and open ocean systems (Block et al., 2011; Ferreira et al., 2015).

Many large shark species undertake oceanic and continental scale movements in response to biological and resource requirements (Heupel et al., 2015). Understanding species movement patterns is necessary to provide insight into predator-prey dynamics of communities and identifying ecosystem consequences that result from the removal of these apex species from systems. Therefore, studies on the movement ecology and behaviour of individuals are increasingly important given the large-scale declines some populations experience (Hammerschlag et al., 2012). However, ecological data on large mobile marine predators such as sharks can be difficult to obtain due to their low abundance, elusive and solitary nature, and the vast spatial ranges many species traverse in what is typically a challenging environment for scientists (Pade et al., 2009; Abrantes & Barnett, 2011; Jewell et al., 2011). In addition, species movement patterns can vary

between sexes and across ontogeny, with some species and life stages displaying strong site fidelity, while others show seasonal movement patterns or large-scale migrations making them difficult to observe for any length of time (Kohler & Turner, 2001; Bruce et al., 2019). Oceanic and deep-water species are particularly difficult to study (Kohler & Turner, 2001). As a result, fisheries-independent information on the movements, habitat requirements, and the role many sharks play in linking and structuring communities remain limited (Pade et al., 2009; Queiroz et al., 2012; Ferreira et al., 2015; Heupel et al., 2015).

Although knowledge gaps remain, the use of conventional and electronic (acoustic and satellite) tagging methods have increasingly expanded our understanding of the behaviour and distribution patterns of a range of shark species, across both varying environments and geographic scales (Kohler & Turner, 2001; Meyer et al., 2010; Fontes et al., 2018). Using such methods, mindful that only a (sampling biased) proportion of a species are tagged, an understanding of movement patterns at an individual level can provide useful insight into the spatial dynamics of the wider population (Jorgensen et al., 2010).

The use of conventional tagging techniques has been adopted for centuries on marine and freshwater species in the form of dyes, branding, mutilation, countable traits, and other morphometric characteristics (Kohler & Turner, 2001). However, physical tags that are attached externally to study individuals with a recognisable component such as an individual serial number are the most commonly used (Kohler & Turner, 2001). External conventional tags have been successfully deployed on sharks since the 1940's in response to concern over declining fisheries catches, and have contributed towards knowledge such as seasonal movement patterns, distance travelled, time at liberty, movement rates, mortality rates, growth rates, and relative population size and dynamics for various species through cooperative tagging programs (Kohler & Turner, 2001). However, despite their extensive use, these tags are limiting as they only provide information on the initial tagging and final recapture position, with no information on movement patterns between the two capture locations received (Francis et al., 2019). Furthermore, the success of conventional tagging studies relies on the deployment of large quantities of tags and sufficient recapture and reporting of previously tagged individuals (Hammerschlag et al., 2012), with low recapture rates commonly reported among the literature (Kohler & Turner, 2001).

Acoustic tagging, where anchored data logging receivers detect coded sound pulses from tag transmitters attached to study individuals when in range of a receiver array, provides greater resolution on the movement patterns of tagged individuals than conventional tagging methods. With the development from short term, labour intensive active tracking methods, to the now more widely used long-term passive tracking technology, acoustic telemetry has been applied to investigate aspects of species ecology such as migrations, home ranges, the use of environmental features, habitat preferences and diel and circadian rhythms across at least 94 different study species (Heupel & Webber, 2012). However, the high costs and logistical constraints involved in setting up and maintaining an acoustic array can limit the size of the study area. While arrays can provide useful information on habitat use and movement patterns of smaller, more resident species, acoustic tracking typically only covers a portion of the range of larger, more mobile species, potentially missing crucial habitat associations (Abrantes & Barnett, 2011). As a result, only inferences on their use of habitat within a particular array can be made, with movement patterns between detections unknown.

Satellite telemetry has revolutionised the way in which scientists track highly mobile marine vertebrates (Hart & Hyrenbach, 2009), with continually improving technologies allowing increased spatial resolution, often elucidating previous misconceptions on aspects of ontogeny and home range size of many marine animals (Hays et al., 2007; Hammerschlag et al., 2012; Heupel et al., 2015; Bruce et al., 2019). Compared to conventional and acoustic tagging methods, satellite tags can provide relatively long-term, near real time tracking data by transmitting broad geographical locations directly to the ARGOS satellite system from anywhere in the world (Francis et al., 2015b). The horizontal movement data received from satellite tags describes "what" an animals movements are (Hammerschlag et al., 2012). Dependent on tag design, tags can also be set to concurrently record biophysical data during travel. Parameters such as depth, ambient water temperature, chlorophyll content, surface intervals, feeding and diving behaviour, swimming speed, and physiological aspects such as body temperature and heart rate of the tagged individual can be recorded (Hays et al., 2007; Hart & Hyrenbach, 2009; Musyl et al., 2011; Hammerschlag et al., 2012; Francis et al., 2015b; Fontes et al., 2018). This information provides an array of supporting behavioural and environmental information potentially determining the "why" aspect of an animal's movements (Pade et al., 2009).

However, this technology is not without limitations. Factors such as tracker unit battery life, and animal behaviour to ensure sufficient surface time of tagged individuals to allow satellite transmission need to be considered when evaluating the suitability of this method (Abrantes & Barnett, 2011). Depending on the objectives of a study, large numbers of tags may also need to be deployed to effectively represent potential differences in movement patterns and habitat use between the different age groups and sexes within a population of interest (Abrantes & Barnett, 2011). Despite such limitations, with the removal of the spatial restrictions and resolution issues that were typical of conventional and acoustic tagging methods, satellite telemetry has allowed the investigation of species movements beyond the coastal region. Satellite telemetry has assisted scientists in understanding ecological concepts such as post-release mortality rates in commercial fisheries (Campana et al., 2009; Afonso & Hazin, 2014); diel depth changes and diving behaviour (Bonfil et al., 2010; Francis et al., 2015b); temperature preferences (Carlson et al., 2010; Hoffmayer et al., 2014); habitat use, and movement and residency patterns (Bruce et al., 2006; Heithaus et al., 2007b; Carlson et al., 2010; Papastamatiou et al., 2010; Queiroz et al., 2012; Vandeperre et al., 2014; Francis et al., 2015a; Bruce et al., 2019; Francis et al., 2019). In addition, behavioural variation with ontogeny (Vandeperre et al., 2014); seasonal movement patterns (Meyer et al., 2010; Bruce et al., 2019) and large-scale migratory pathways and patterns, including transoceanic migration (Bonfil et al., 2005; Bonfil et al., 2010; Campana et al., 2011; Duffy et al., 2012; Domeier & Nasby-Lucas, 2013; Francis et al., 2015b) of both coastal and pelagic species can be identified. Furthermore, the adaptive design of such tags has allowed for the tagging of a diverse range of species such as sea turtles, tunas, billfishes, sharks, marine mammals and sea birds such as albatrosses (Hays et al., 2007; Heithaus et al., 2007b; Hammerschlag et al., 2012).

With rapid declines in global shark populations increasingly demonstrated, attaining sufficient data on how these often highly mobile animals utilise such a diversity of seascapes remains a high priority to inform conservation management (Hammerschlag et al., 2012). The development of sophisticated telemetry presents a key tool for understanding the often wide spread and complex spatial organisation of shark species, with sustained, long-term monitoring being crucial in the collaborative development and prioritisation of appropriate management and conservation strategies of species, often across multiple jurisdictions (Vandeperre et al., 2014; Ferreira et al., 2015; Bruce et al., 2019). Furthermore, satellite telemetry supports resource management questions

addressing the overlap of species' oceanographic habitats with anthropogenic activities such as fisheries, and oil and gas exploitation (Hart & Hyrenbach, 2009). As expected, satellite telemetry is now considered common practice among the scientific community (Bruce et al., 2019).

Bronze whaler sharks (*Carcharhinus brachyurus*) have been shown to move large distances, up to 2315 km (Cliff & Dudley, 1992; Rogers et al., 2013), with strong site fidelity and habitat utilisation within coastal areas during the summer months being detected in many populations across their range (Smale, 1991; Cox & Francis, 1997; Lucifora et al., 2005; Drew et al., 2019). However, their seasonal location throughout the winter months has not yet been verified and thus, it cannot be determined if true seasonal migration with subsequent return to coastal habitats occurs in this species. To date, satellite telemetry technologies have not been used to investigate the spatiotemporal movement patterns of bronze whaler sharks, with descriptions of seasonal trends and the distribution of this species being primarily described through conventional tag and release programs, assessment of catch in beach protection nets and fisheries information (Cliff & Dudley, 1992; Rogers et al., 2013). More recently, a study in the Gulf of St Vincent, Australia, reported the first use of acoustic telemetry in this species documenting habitat preference and seasonal use of the gulf within an extensive receiver array (Drew et al., 2019). However, the movements beyond the gulf during winter remained unknown (Drew et al., 2019).

This chapter presents results from the first use of satellite tracking to investigate the movement ecology of bronze whaler sharks. Two satellite-linked smart position or temperature transmitting (SPOT5) tags were donated to the study by Malcolm Francis (National Institute of Water and Atmospheric Research - NIWA) after being excess from prior research on white sharks (*Carcharodon carcharias*). These tags provided the opportunity for an exploratory investigation with the objectives to:

1) Test the efficacy of SPOT5 tags in providing spatiotemporal data on bronze whaler sharks for which surfacing behaviour is unknown
2) Obtain preliminary insights into the long-term movement patterns of bronze whaler sharks in New Zealand at a spatial scale of up to tens of kilometres, and over time periods of days to months

3) Identify if temperature is an environmental factor influencing the seasonal movement patterns of this species

It is hypothesised that tagged bronze whaler sharks will show movements away from shelf habitats such as coastal areas and nearby offshore islands during the austral winter months of July until September, and that temperature will be a driving factor in the coastal residency patterns of this species. Because bronze whaler sharks have not been studied in this manner elsewhere, some of the findings of this study were discussed against studies on other Carcharhinid species of a similar size for comparison.

2.2 Methods

2.2.1 Study Site

The Bay of Plenty region is located along the north-eastern coastline of New Zealand and has a warm temperate maritime climate (Figure 2.1A, B). With a narrow continental shelf ~50 km wide, the Bay of Plenty is influenced by the East Auckland Current which injects subtropical waters from the East Australian current into the region (Stevens et al., 2019). As a result, inshore water temperatures range from 13.1°C to 16.3°C during winter, and 17°C to 24.2°C during summer (https://envdata.boprc.govt.nz/Data). The diversity of habitats such as estuarine, rocky and sandy coastlines, inshore and offshore islands, and continental shelf slope, along with the physical conditions of the region support a range of biological communities along with a lucrative commercial and recreational fishery. North of the Bay of Plenty and with a similar oceanic climate are the Hauraki Gulf and Auckland region zones (Figure 2.1A, B). Also with a narrow shelf 20–30 km wide, these regions are further known for their clusters of extensive island groups (Stevens et al., 2019), and also support diverse and productive ecosystems (Peters et al., 2020). With offshore sea surface temperatures ranging from 15°C in winter to 22°C in summer, and inshore temperatures from 16.5°C to 21°C (Stevens et al., 2019), the Hauraki Gulf, Auckland and Bay of Plenty zones provide a continuous environment allowing large-scale movements of wide-ranging marine species along the north-eastern coast of New Zealand, with minimal restriction of geographical barriers.

2.2.2 Capture, tagging and release of sharks

Two female bronze whaler sharks were captured during May, 2017, using rod and reel, land-based from Panepane Point, Matakana Island, at the southern entrance to the Tauranga Harbour (Figure 2.1C). This location was selected based on its accessibility and high capture success in previous research expeditions. At this site, the bathymetry quickly drops to depths of 14–25 m due to high water movement and excavation of the shipping channel. Sharks are known to travel around this point along the edge of the deeper channel as they enter the expansive harbour system, with game fishermen typically targeting the species during high tide times to coincide with shark movements into the harbour with the incoming tide. Furthermore, targeting sharks at this location confirmed tagged individuals were still utilising coastal areas toward the end of the austral summer period.

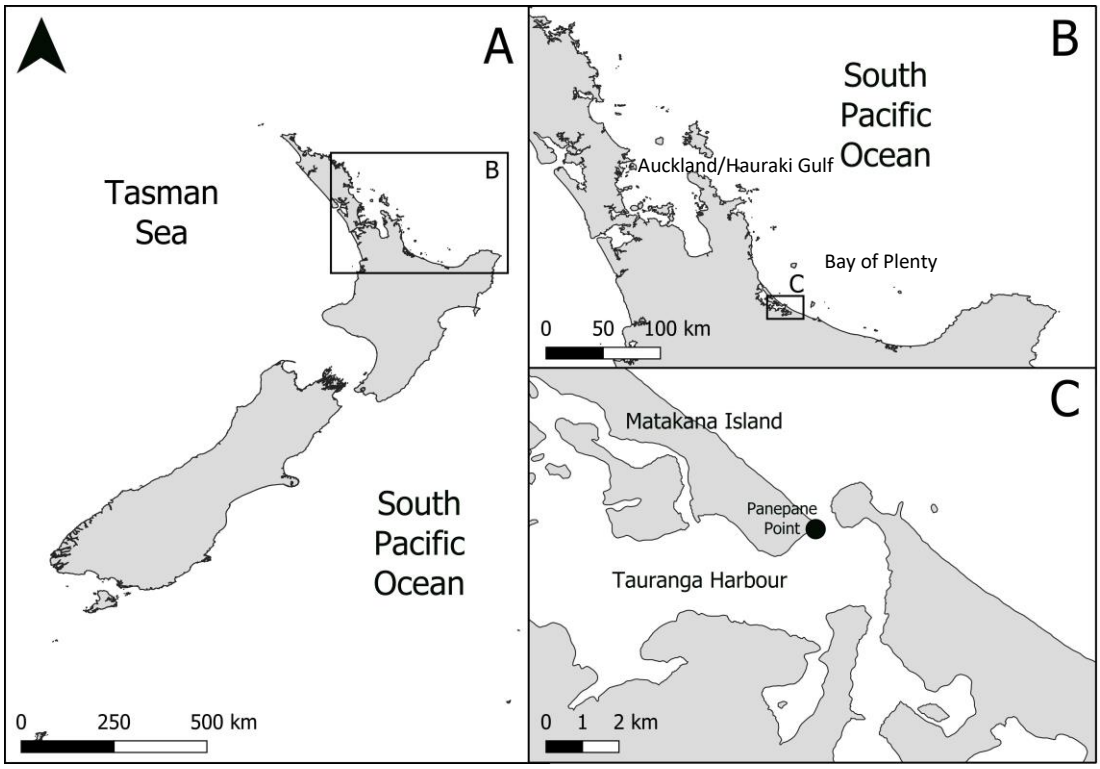

Figure 2.1: Study area showing A: North-eastern region of New Zealand; B: Bay of Plenty, Hauraki Gulf and Auckland study regions mentioned in the text; C: Capture and tagging location (indicated by black circle) of bronze whaler sharks (*Carcharhinus brachyurus*) at Panepane Point, Matakana Island (-37.638°S / 176.162°E). Map produced using Quantum GIS (v3.16, Hannover). Spatial data obtained from DIVA-GIS. CRS: WGS84 (EPSG 4326).

Sharks were caught using a Triton Beast Master 4/0 Shimano big game trolling reel and Shimano IGFA 15 kg Stroker rod. Whole, large bonito (family Scombridae) were used as bait. Tackle included Maui SS 16/0 long shank stainless steel circle hooks, with a 10

m long 600 lb monofilament leader, which had a 0.5 m long double twist at the hook end for extra strength against possible shredding caused by the teeth of the shark. At the opposite end, this leader clipped onto a swivel at the base of a 7.62 m wind-on leader composed of Momoi's Hi-Catch X-Hard 2.05 mm diameter, 400 lb nylon monofilament, which sequentially attached to 100 m of 37 kg Berkley big game nylon overlying 90 lb braid which comprised the remainder of the line on the reel. All gear was set up professionally at a local fishing outlet, and regularly checked and maintained at a high standard of integrity to avoid any preventable breakages during future captures.

Once hooked and reeled in to shallower water, the captured shark was guided into the shoreline by an experienced game fisherman drawing on the leader where it was temporarily removed from the water so the sampling and tagging procedure could be performed. Once ashore, sex of the shark was determined by the presence or absence of claspers at the pelvic fins. From the tip of the snout, the pre-caudal (PCL), fork (FL), and total length with the tail in a flexed position so the upper lobe lay along the midline of the body (TL_{flex}) were measured to the nearest 0.5 cm over the curve of the dorsal surface of the body (see Chapter 3, Section 3.2.1.2). Assumptions of sexual maturity were based on total length measurements. In addition, a fin clip was taken from the posterior margin of the first dorsal fin and stored in 95% ethanol for future genetic analysis, and a tissue biopsy was taken from the right dorsal musculature below the first dorsal fin, and kept on ice until stored at -20°C for use in later stable isotope analysis. Satellite-linked smart position or temperature transmitting tags (SPOT5; Wildlife Computers Ltd, Redmond, Washington, USA) (n = 2) were attached to the anterior region of the first dorsal fin where the fin was the thickest. A predrilled template was used to initially drill four holes through the fin using a 6 mm drill bit. The tag was then secured at the bottom by two marine-grade stainless steel 50 mm bolts and ¼" nyloc nuts and washers, and tightened using the drill and vice grips. This process was repeated for the two top holes of the tag, but using 30 mm bolts due to the upper region of the fin being thinner towards the apex. The tag was positioned high near the apex of the first dorsal fin to ensure maximum height of the antennae for optimal signal transmission when the sharks fin breached the waters surface. The back surface of the tag, which lay adjacent to the fin, was neoprene-lined to prevent damage such as rubbing and irritation to the fin. Prior to deployment, anti-fouling paint was also applied to all areas of the tag to minimise biofouling, with the exception of the saltwater

switch and antennae so as not to interfere with transmissions (Jewell et al., 2011). A conventional Ministry for Primary Industries (MPI) Gamefish stainless steel dart tag also was inserted into the left dorsal musculature at the base of the first dorsal fin for secondary identification, and to allow recaptures to be reported to the wider MPI tag and release program.

Location, date, and time of capture, landing and release were also recorded. Further information such as mating scars, pigmentation, parasites and temperament of the shark were recorded, and females were noted for possible pregnancy based on the size of their abdomen. However, this could not be accurately determined by just our visual observation, with an ultrasound or dissection being required to attain confirmation, but were unable to be performed in this study. Once the tagging and sampling procedure was completed, the hook was removed or cut using bolt cutters and the shark was released alive, being held in the water until it swam away without assistance. The condition of the shark on release was assessed on a continuum from 0–5, with 0 representing death and 5 indicating the shark swam away strongly. Angling times varied depending on tidal conditions and how the shark responded to capture. However, the sampling and tagging procedure took no longer than 11 minutes.

2.2.3 Data Analysis

2.2.3.1 Geo-Location

Real time, satellite derived position estimates of each shark were communicated via the ARGOS satellite system, relying on the sharks' dorsal fin to break the surface for a long enough duration for the conductivity sensors to detect the antenna to be temporarily dry to initiate signal transmission to an orbiting satellite (Meyer et al., 2010). Tags were pre-programmed to transmit a maximum of 200 transmissions per day. Tags were also enabled to transmit 23 hours in a day and on every day of each month using an absolute calendar year. A default wet / dry threshold value of 50 was used to determine when the saltwater switch was "wet" vs. "dry" to initiate transmissions. The transmission interval of tags was set to a fast repetition rate of 45.50 seconds and a slow repetition rate of 90.50 seconds. However, the slow repetition rate for when the tag was exposed above the waters surface was disabled. Tags checked for dry conditions every 0.25 second and were set to transmit after one extra consecutive dry 0.25 second interval, resulting in a 0.5 second delay in transmission upon surfacing. Spatial precision of transmissions

were coded as one of seven location class (LC) categories based on the estimated radius of error calculated from Doppler shift measurements of the transmission frequency and repetition period of the data stream received (https://www.argos-system.org/argos/how-argos-works/). From most to least accurate, location class 3 has an accuracy of <250 m; class 2, 250–500 m; class 1, 500–1500 m; class 0, >1500 m; class A and B, no accuracy estimation provided although have been reported to be within a few kilometres of true position (Bruce et al., 2006); and class Z, invalid location (Argos, 2016). All transmissions with location classes 3, 2 and 1 were accepted for analysis. Locations of classes 0, A or B were used only when their location was within a rational distance from the previous position estimate. Locations with Z location class codes or on land were discarded. The filtering of position estimates with unreliable location classes removed 24% (8 out of 34 total transmissions) of the available data. The number of detections per day was calculated by dividing the total number of detections by the number of days in the transmission period. Maps of movement tracks for each shark were generated using R software. Transmitted locations were colour coded by month of the year and classified by austral seasons: spring = October to December; summer = January to March; autumn = April to June; and winter = July to September (Francis et al., 2015b). Our particular interest was in the movements of the tagged bronze whaler sharks during the winter period, and if their movements remained in shelf habitats, defined as waters <200–250 m depth (Francis et al., 2015b; Stevens et al., 2019), or if they moved further offshore into oceanic waters beyond the continental shelf.

2.2.3.2 Movement Metrics

For each shark, the range of latitudinal distance travelled was calculated by subtracting the latitude of the northernmost transmission from the latitude of the southernmost transmission. This produced the metric Δ_{LAT} (Bruce et al., 2019). The same metric was calculated for longitude by subtracting the easternmost transmission from the westernmost transmission, producing Δ_{LONG}. Minimum straight-line distances travelled (km) by each shark was estimated by measuring vectors between each transmission location to the nearest 10 m using an online co-ordinate distance calculator (http://boulter.com/gps/distance/). The total minimum straight-line distance travelled was the sum of these consecutive vectors from the deployment location to the location of the final reliable transmission before communication with each tag ceased. Mean daily distance travelled (km) was calculated by dividing the total minimum straight-line

distance by the number of days in the transmission period. The distance between the tagging location and the transmission location furthest from this point was also measured, and reported as the maximum distance from the tagging location. Minimum swim speeds for each shark were also estimated in km/h and m/s using the calculated distances and times (converted from Coordinated Universal Time (UTC) to New Zealand Standard Time (NZST = UTC + 12)) between each transmission location using the formula S = D / T, where S = speed, D = distance between transmissions and T = the time it took to travel between each transmission. Speed as a factor of shark length was also calculated by dividing the speed in m/s by TL_{flex} in meters.

2.2.3.3 Temperature Data

Satellite tags were programmed to record and temporarily archive ambient water temperature at 10 second intervals within a range of <8–>28°C. Time at temperature histograms were provided by the tag which summarised the fraction of the histogram period the animal spent within the following 12 pre-defined temperature bins: <8, 8–10, 10–12, 12–14, 14–16, 16–18, 18–20, 20–22, 22–24, 24–26, 26–28, and >28°C. Histogram duration was set to 12 hours, creating two time-at-temperature histograms per day. Because the tag transmission buffer can store up to 12 messages, temperature information communicated from the tags represented ambient temperatures encountered six days prior to transmission. Percentage dry timelines to indicate the percentage of time spent dry for each hour of the day was disabled to reserve battery capacity. Approximate temperature of inshore areas when sharks departed to offshore environments were estimated by simultaneous examination of sea surface temperature data sourced from the Bay of Plenty Regional Council Environmental Data Portal (https://envdata.boprc.govt.nz/Data). Temperature data was recorded by the Bay of Plenty Regional Council from a surface data logger buoy located 13 km offshore, mid Bay of Plenty.

Throughout this chapter, standard deviation (SD) was provided to indicate variance around the mean, unless otherwise specified.

2.2.4 Ethics statement

The work undertaken in this project was approved by the University of Waikato Ethics committee Protocol #974. This research did not involve interaction with threatened or

protected species. Furthermore, no animals were sacrificed in the study, and procedures were put in place to ensure replacement, reduction and refinement to minimise any impact on the study animals. As a result, this research was considered to have moderate impact on the study species.

2.3 Results

2.3.1 Tag Performance

Two female bronze whaler sharks were successfully tagged with SPOT5 tags from Panepane Point, Matakana Island, at the entrance to the southern Tauranga Harbour, Bay of Plenty. Both sharks were hooked in the corner of the jaw and swam away in strong condition (condition index 4). Sharks were tagged at the beginning of the austral autumn. Shark ID 55617 was tagged on 1st April, 2017, and measured 297 cm TL_{flex}. Shark ID 55620 was tagged on 8th April, 2017, and measured 286 cm TL_{flex}. Based on previously established size at maturity for female bronze whaler sharks (215–271 cm TL; Garrick, 1982; Smale, 1991; Walter & Ebert, 1991; Lucifora et al., 2005; Drew et al., 2016), both sharks were considered mature. Summary data for each tag was transmitted via the Argos satellite system and included geolocation estimates for latitude and longitude, and time-at-temperature data. Both sharks transmitted valid geolocations allowing the evaluation of each movement track. Tagging performance was fair, with 50% of locations overall having a location class of either 1, 2 or 3, indicating that 50% of locations were within 1500 m of true positions, and 50% having location classes A or B where no estimation of accuracy was provided. Locations of class 0 (n = 2) were removed prior to analysis and class Z were not available from Argos (Table 2.1). However, the total number of transmissions received was low, with 11 for shark 55617 and 13 for shark 55620 (not including tagging location estimate), providing location estimates on only 5% and 8% of days respectively during the transmission period (Table 2.2). As a result, the number of detections per day were only 0.07 for shark 55617 and 0.09 for shark 55620.

Table 2.1: Performance details of satellite-linked smart position or temperature transmitting (SPOT5) tags secured to two mature female bronze whaler sharks (*Carcharhinus brachyurus*) in New Zealand. Values show number of location estimates in each location class out 11 transmissions for shark ID 55617, 13 for shark ID 55620, and a total of 24 transmissions overall for both sharks combined.

ARGOS Location Class	3	2	1	0	A	B	Z	Total
Uplinks needed for fix*	≥4	≥4	≥4	≥4	3	≤2	-	
Accuracy (m)*	<250	250-500	500-1500	>1500	-	-	-	
Shark 55617 transmissions	1	3	2	0	2	3	0	11
Shark 55620 transmissions	2	1	3	0	3	4	0	13
Combined transmissions	3	4	5	0	5	7	0	24

*Argos (2016)

2.3.2 Geographic movements

2.3.2.1 Shark ID 55617

Shark 55617 (Figure 2.2; Appendix 1) had a total track duration of 156.98 days, over an estimated total straight-line distance of 363.49 km before transmissions ceased on 5th September, 2017 (Table 2.2). The shark was at liberty for 38.64 days before its first transmission at the top of the Coromandel Peninsula near the northern end of Rauporoa Bay, 137.8 km north-west of its tagging location. Three more transmissions within 12 km of this location were received in <50 m water depth on 12th May, 2017, as the shark travelled south along the rocky stretch of coastline from Rauporoa Bay to the sandy Waikawau Bay. The short distances and longer periods of time between these locations suggest the shark was not in transit between locations, but instead utilising the area for purposes such as foraging. The next transmission was not received until 17th May, 2017, 75.22 km south-east in approximately 100 m water between the Whangamata Coastline and Tuhua Island. Three more transmissions were received in this region between 18th and 19th May, 2017, in an easterly direction. There was a change in behaviour between 20th June and 5th September during late autumn and winter, where locations went from coastal and shelf-associated (<100 m) to remaining within a restricted area along continental shelf-edge waters in June and July. The final transmission received 5th September, 2017, was from off the shelf-edge in ~500 m depth, 72.2 km north of the previous July location. The lack of further transmissions

prevented our ability to determine a seasonal return to the shallower coastal area the following summer. However, shark 55617 was recaptured 539 days after tagging and identified through photo identification on 23rd September, 2018, at Panepane Point where it had been initially tagged. The tag was still attached, but was in the process of dislodging from the dorsal fin and the aerial and unit were covered in fouling. This recapture indicated a return to nearshore coastal environments. Overall, the shark ranged over 1.138° latitude and 0.975° longitude, with the greatest distance from its tagging location measuring 137.84 km. The mean daily distance travelled was 2.32 km.

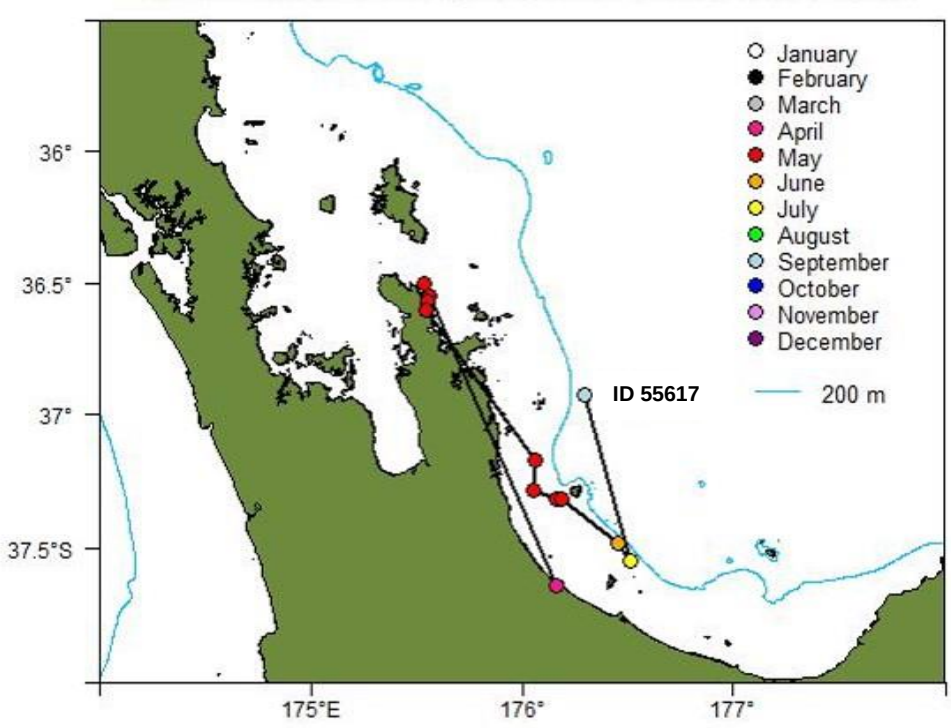

Figure 2.2: North-eastern region of New Zealand showing tracks of one of two bronze whaler sharks (*Carcharhinus brachyurus*) (ID 55617) tagged with satellite-linked smart position or temperature transmitting (SPOT5) tags in 2017. Transmission locations are colour coded by month of the year. Blue line indicates the edge of the continental shelf at 200 m depth.

2.3.2.2 Shark ID 55620

Shark 55620 (Figure 2.3; Appendix 2) had a total track duration of 145.34 days, over an estimated total straight-line distance of 568.45 km before transmissions ceased on 31st August, 2017 (Table 2.2). The shark was at liberty for 11.43 days before its first transmission on 19th April, 2017, off the Bowentown coastline in ~30–50 m water depth, just 20.51 km north of its tagging location. The shark remained in this area with two further transmissions on the 19th and 21st April within 3.26 km of this location.

Eighteen and 20 days later, two transmissions were received during May, 24 km and 30.39 km respectively, south-east along the same stretch of coastline at locations near Motiti Island. All autumn transmissions received during April and May remained in <50 m water depth.

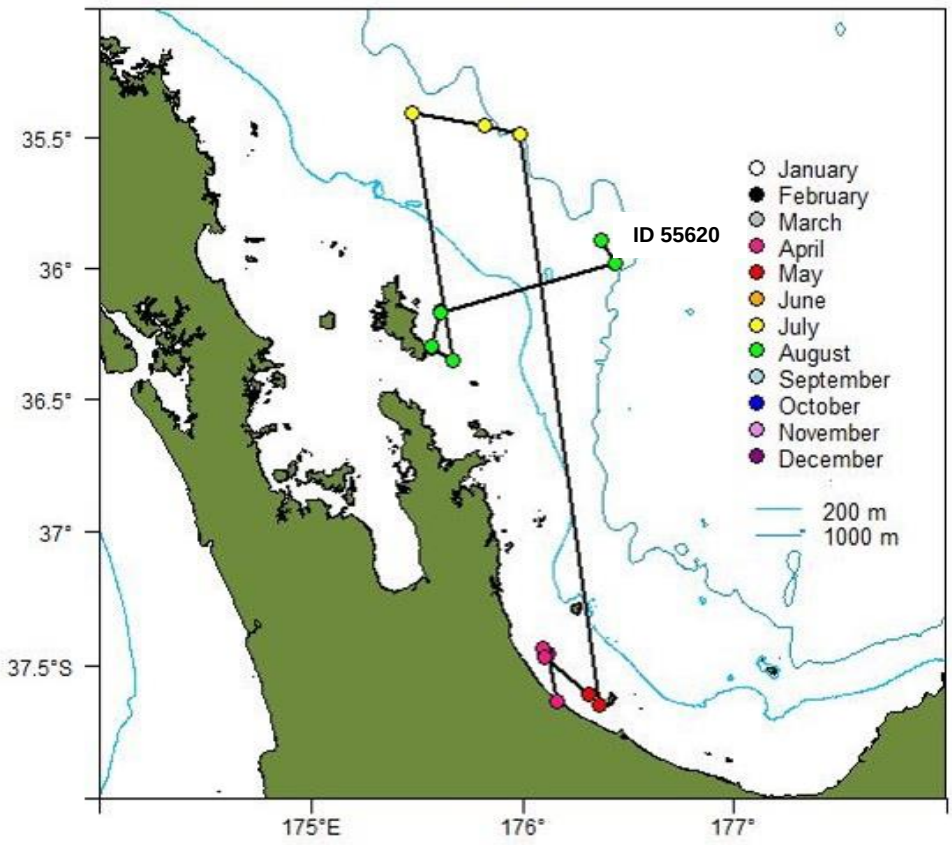

Figure 2.3: North-eastern region of New Zealand showing tracks of one of two bronze whaler sharks (*Carcharhinus brachyurus*) (ID 55620) tagged with satellite-linked smart position or temperature transmitting (SPOT5) tags in 2017. Transmission locations are colour coded by month of the year. Blue lines indicate the edge of the continental shelf at 200 m depth and the 1000 m depth contour.

No transmissions were then received until winter in July, which also coincided with a change of behaviour. Shark 55620 transmitted 242.34 km north of its previous location off the continental shelf in 1000 m of water. Three transmissions were received in this deeper oceanic region on the 21st, 27th and 29th July in waters no less than 500 m in depth. On 8th August, the shark transmitted three locations back in shelf waters between ~50–100 m depth, just east of Great Barrier Island. This was followed by a directed movement east, back into oceanic waters with two further locations in ~1000 m depth before transmissions ceased. Overall, the shark ranged over 2.245° latitude and 0.958°

longitude, with the greatest distance from its tagging location measuring 255.29 km. The mean daily distance travelled was 3.91 km.

Table 2.2: Summary of satellite-linked smart position or temperature transmitting (SPOT5) tag tracking data for bronze whaler sharks (*Carcharhinus brachyurus*) deployed at Panepane Point, Matakana Island, at the entrance to southern Tauranga Harbour, New Zealand.

Shark ID	TL_{flex} (cm)	Sex	Mature*	Tagging Date	Tagging latitude	Tagging longitude
55617	297	Female	Y	1/04/2017	-37.638	176.162
55620	286	Female	Y	8/04/2017	-37.638	176.162

Shark ID	Date of last transmission	Transmission period (days)	Total number of detections	Number of days detected n (%)	Detections per day
55617	5/09/2017	156.98	11	8 (5)	0.07
55620	31/08/2017	145.34	13	11(8)	0.09

Shark ID	Total minimum straight-line distance (km)	Mean daily distance travelled (km)	Maximum distance from tagging location (km)	Δ_{LAT} (°)	Δ_{LONG}(°)
55617	363.49	2.32	137.84	1.138	0.975
55620	568.45	3.91	255.29	2.245	0.958

TL_{flex} = Total length with the tail in a flexed position along the midline of the body
*Maturity status was based on previously established size at maturity for female bronze whaler sharks (215–271 cm TL; Garrick, 1982; Smale, 1991; Walter & Ebert, 1991; Lucifora et al., 2005; Drew et al., 2016)

2.3.2.3 Swimming Speed

Minimum swimming speeds were estimated for each bronze whaler shark from point-to-point displacement distances within each track. Displacement distances ranged from 2.48 km to 242.34 km. Travelling time between points ranged from 0.68 hours and 1679.92 hours. Estimates of minimum swimming speed calculated for each movement vector for shark 55617 ranged from 0.03 km/h to 3.63 km/h, with a mean minimum swimming speed of 0.75 km/h (Table 2.3; Appendix 1). Slow swim speeds were produced by vectors of a short distance, with a long time period. Therefore, these were not considered true estimates of minimum swimming speed as movements between these points were not determined. A minimum swim speed of 3.63 km/h was the most accurate estimate for shark 55617, as it was calculated from two transmissions in a directed movement 2.48 km and 41 minutes (0.68 hours) apart. Furthermore, these

transmissions had a location class of 2 and 1, providing a high level of accuracy in position estimates. Estimates of minimum swimming speed for shark 55620 ranged from 0.03 km/h to 6.54 km/h, with a mean minimum swimming speed of 0.99 km/h (Table 2.3; Appendix 2). A minimum swim speed of 3.06 km/h was considered the most accurate estimate, calculated between two location transmissions 3.26 km and 1 hour and 4 minutes (1.07 hours) apart. Both transmissions had a location class of 1, and thus, also provided a higher level of known location accuracy.

Table 2.3: Estimated minimum swimming speeds of two bronze whaler sharks (*Carcharhinus brachyurus*) tagged with satellite-linked smart position or temperature transmitting (SPOT5) tags in north-eastern New Zealand. Minimum swimming speeds ranged from 0.03 km/h to 3.63 km/h for shark 55617, and 0.03 km/h to 6.54 km/h for shark 55620. The point-to-point displacement speeds presented were selected based on assumed directed movement between two transmission locations with accuracy classes 1 or 2.

Shark	TL_{flex} (cm)*	km/h	m/s	TL/s
55617	297	3.63	1.01	0.34
55620	286	3.06	0.845	0.30

* TL_{flex} = Total length with the tail in a flexed position along the midline of the body

2.3.2.4 Temperature

Satellite tags provided 101 time-at-temperature histograms between 7th April, 2017, and 8th January, 2018. Geolocation data was not always transmitted with temperature information. Sharks 55617 and 55620 both occupied a wide range of ambient water temperatures between 12°C and 22°C (Figure 2.4; Appendix 3 and 4). However, a narrower temperature preference for both sharks was identified. Shark 55617 spent 40.10% of its time at 16–18°C, and 42.43% between 18–20°C. Shark 55620 spent 44.93% of its time at 16–18°C, and 45.26% between 18–22°C.

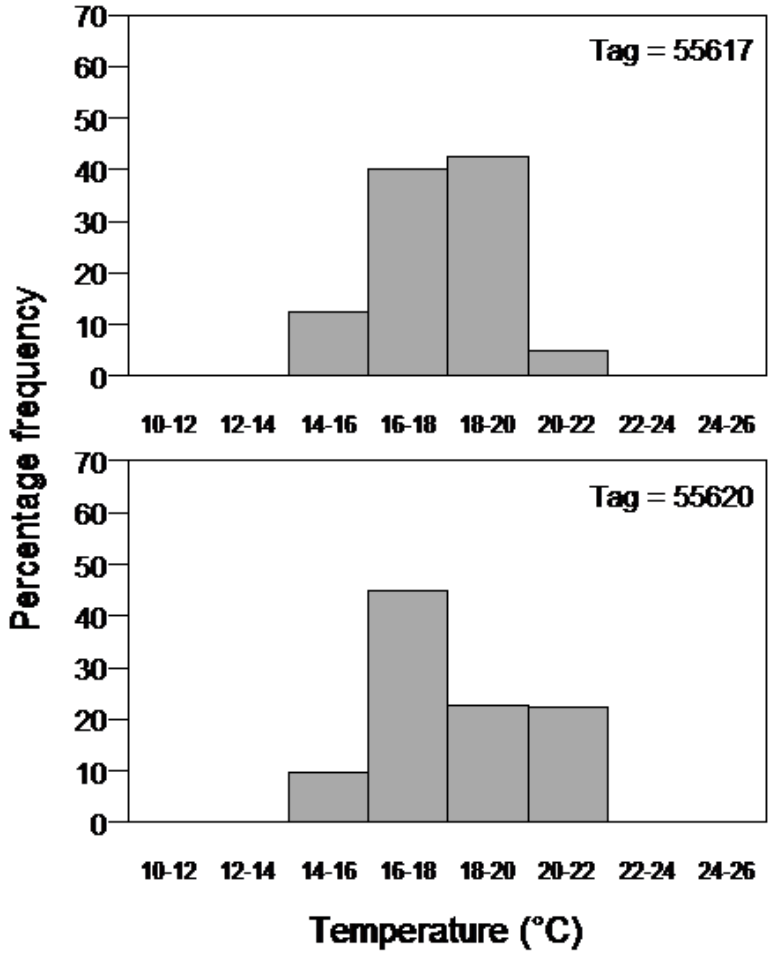

Figure 2.4: Percent time spent within pre-specified temperature bins by two mature female bronze whaler sharks (*Carcharhinus brachyurus*) tagged with satellite-linked smart position or temperature transmitting (SPOT5) tags in north-eastern New Zealand. Data presented is a summary of time-at-temperature histogram data received between 7th April, 2017, and 8th January, 2018. Because percentage time spent between 12–14°C was minimal for each shark, it did not present on the histogram, but was equal to 0.06% for shark 55617, and 0.01% for shark 55620.

When investigating temperatures over time on a monthly basis, both sharks experienced declining water temperatures as the winter period approached (Figure 2.5). The majority of ambient water temperatures during autumn (April–June) were between 16–20°C for shark 55617, and 18–22°C for shark 55620. The lower temperature range experienced by shark 55617 was due to no temperature data being received by shark 55620 in June as water temperatures declined. Ambient water temperatures during winter (July–September) did not exceed 18°C for either shark, and very rarely dropped below 14°C. During this period, shark 55617 remained almost exclusively at temperatures between 14–18°C, while shark 55620 spent the majority of its time between 16–18°C. It cannot be determined exactly when the sharks moved into shelf-edge and oceanic habitats due to unknown movement patterns between transmissions. However, measurements by a local surface buoy indicated that coastal temperatures

were ~16.6°C when shark 55617 first reported on the shelf-edge on the 20th June, 2017, and coastal temperatures of ~15.1°C when shark 55620 first reported in oceanic habitats on 21st July, 2017.

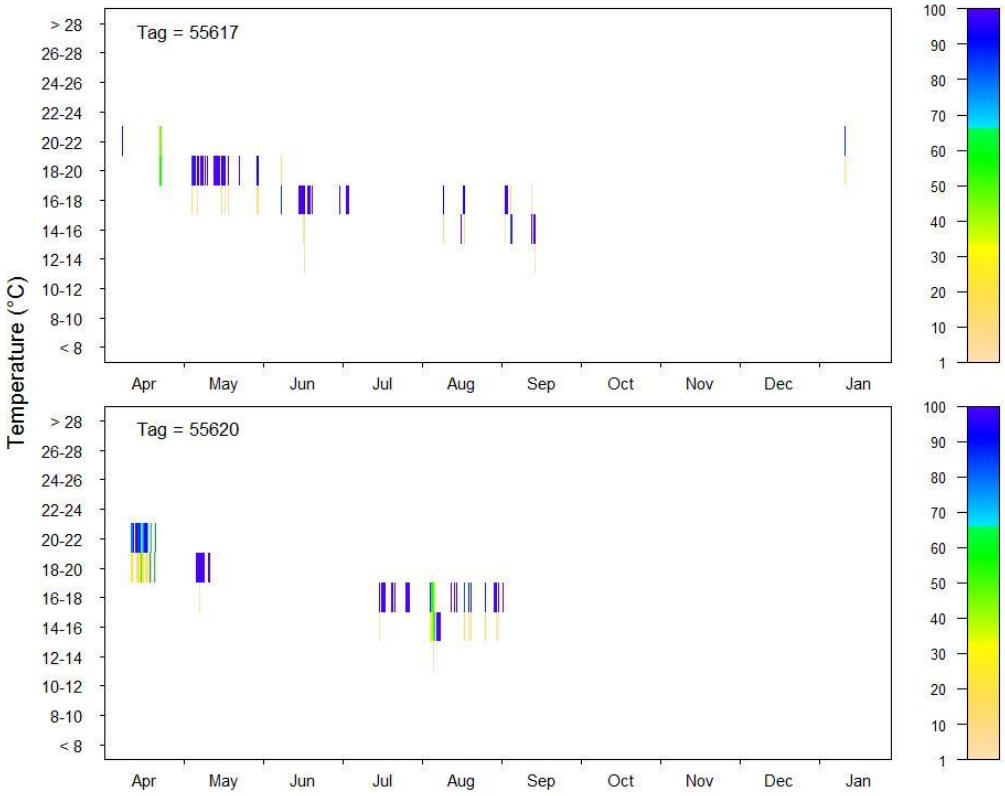

Figure 2.5: Percent time (right axis) spent in 12 pre-determined temperature bins (left axis) by two mature female bronze whaler sharks (*Carcharhinus brachyurus*) tagged with satellite-linked smart position or temperature transmitting (SPOT5) tags in north-eastern New Zealand. Temperature data was summarised into 12-hour time bins, with up to six days' worth of data being communicated with each successful transmission.

Coastal waters measured by the surface buoy during the winter period averaged 14.89 ± 0.51°C (Figure 2.6). The minimum recorded temperature during this period was 13.8°C, and the maximum 16.2°C. The lower temperatures (14–16°C) experienced by shark 55620 in early August coincided with its return to Great Barrier Island, with the remaining temperatures between 16–18°C indicative of positions in warmer, more stable oceanic habitats. In comparison, the wider temperature range of shark 55617 (14–18°C) could be a result of remaining along shelf-edge regions. The minor amount of time spent in temperatures between 12–14°C could be an indication of diving behaviour. However, this cannot be determined in this study without depth sensor or temperature profile data. The temperature and position data received from both sharks confirm that they did not migrate to tropical regions during the winter months. The

coastal water temperature on 23rd September, 2018, when shark 55617 was recaptured at Panepane Point was 15.4°C. Mean water temperature during the 2018 winter period measured 14.63 ± 0.45°C.

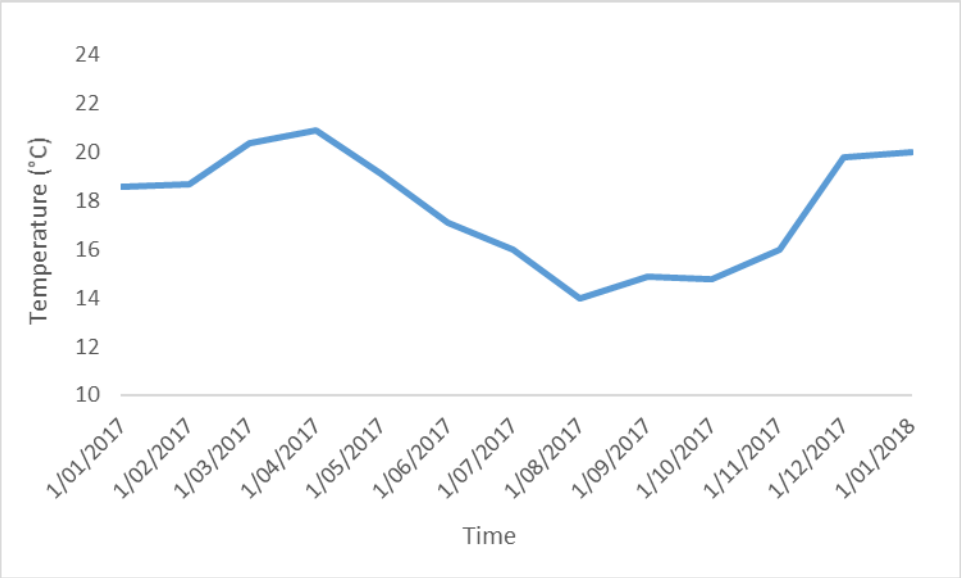

Figure 2.6: Coastal water temperatures measured in the Bay of Plenty by a surface wave buoy, 13 km off the Pukehina coastline in 62 m water depth. Data sourced from the Bay of Plenty Regional Council Environmental Data Portal (https://envdata.boprc.govt.nz/Data).

2.4 Discussion

This study reports on results from the first deployment of satellite-linked tags on bronze whaler sharks, providing novel insights into the movement behaviour of this species in New Zealand waters. However, the results reported here are representative of mature female bronze whaler sharks only, and cannot be assumed to represent the male and juvenile proportion of the population. An understanding of movements of the wider population requires an expansion of tagging across both sexes and different stages of ontogeny, which was not possible in this study. As only two satellite tags were available, the sample size is acknowledged as being low, hence the study should be considered exploratory. It is noted however, that low sample size is the norm for investigations on high range pelagic sharks.

2.4.1 Tag Performance

Information received from SPOT transmitters often provides low spatial resolution due to the limited number of location estimates and the uncertainty of movements of tagged individuals between transmissions (Ferreira et al., 2015). Despite this, satellite tags

continue to successfully elucidate new information on the movement behaviour of marine animals, including various species of sharks. When in comparison to the literature, the performance of tags in this study varied depending on the metric being used for evaluation. Most commonly, the transmission period in days is reported. In this study, shark 55617 and 55620 had a transmission period of 156.98 and 145.34 days respectively. This was comparable to transmission times of fin mounted SPOT tags found in tiger sharks (*Galeocerdo cuvier*) (154.67 ± 188.50 days, n = 6; Ferreira et al., 2015), and exceeded those reported for blue sharks (*Prionace glauca*) (96.6 ± 64.76 days, n = 5; Stevens et al., 2010), bull sharks (*Carcharhinus leucas*) (116.63 ± 69.56 days, n = 16; Hammerschlag et al., 2012), and Galapagos sharks (*Carcharhinus galapagensis*) (71.67 ± 34.31, n = 3; Meyer et al., 2010). Transmission times of this study also exceeded two earlier studies on tiger sharks which reported transmission periods of 78.6 ± 53.99 days (n = 5; Meyer et al., 2010) and 19.33 ± 16.44 (n = 3; Werry et al., 2014). This indicated the tags attached to bronze whaler sharks in this study performed well against multiple studies. Furthermore, the results suggest that bronze whaler sharks can survive being removed from the water for a short period of time to allow tagging before being returned to the sea. However, transmission times fell short of those reported for shortfin mako sharks (*Isurus oxyrinchus*) (259.09 ± 128.34 days, n = 11; Francis et al., 2019), and additional studies on blue sharks (286.74 ± 196.98 days, n = 19; Vandeperre et al., 2014), and tiger sharks (173.83 ± 123.66 days, n = 12; Fitzpatrick et al., 2012).

When evaluating the percentage of days tracked out of the total transmission period, the sharks in this study were detected for only 5% (55617) and 8% (55620) of the transmission time, compared to a mean of 88 ± 9.78% reported in blue sharks (Vandeperre et al., 2014). Furthermore, the number of detections per day in this study were <0.10 compared to 2.24 ± 1.75 (n = 12; Fitzpatrick et al., 2012) and 0.73 ± 0.59 (n = 6; Ferreira et al., 2015) reported for tiger sharks, and 1.07 ± 0.71 (n = 19) reported for blue sharks (Vandeperre et al., 2014). It is assumed that the low detection rates reported for bronze whaler sharks was a product of less time spent at the surface compared to other species. For example, when assessing detection rates of whale sharks where SPOT tags were attached by a tether to the dorsal musculature, mean detections per day were much higher, reporting 6.79 ± 2.64 (n = 15; Rohner et al., 2018), 4.8 ± 0.52 (n = 8; Diamant et al., 2018), and 2.25 ± 0.47 (n = 17; Araujo et al., 2018) detections per day, which could be a reflection of feeding behaviour near the surface in this species.

However, variability around these values is evident indicating that surface behaviour can vary considerably within and between species. The only papers to document the proportion of transmissions in each location class were that of Heithaus et al. (2007b) and Hammerschlag et al. (2012). Heithaus et al. (2007b) reported that only 24.1% of transmissions had a location class of 3, 2 or 1, with only 17.82% being reported by Hammerschlag et al. (2012). This was compared to 50% in this study, suggesting that when bronze whaler sharks did surface, it was often for long enough duration to transmit locations of higher accuracy.

The reason for loss of transmission in this study was unknown. There are a number of factors within the marine environment that can contribute towards tag failure such as battery exhaustion, aerial damage, predation, human error, components of tag assembly, saltwater switch failure and biofouling (Hays et al., 2007; Musyl et al., 2011). Furthermore, it is often difficult to discriminate if a cease in transmissions is a result of equipment failure or death of the animal (Musyl et al., 2011). However, the recapture of shark 55617, 382 days after its final location estimate, confirmed that death was not the cause for at least this shark. The short convalescence period after tagging (11 days), and retrieval of movement data in the months following also suggest that shark 55620 survived the tagging process, and that the cease in transmissions was a result of a different factor. However, we cannot rule out the possibility of predation following the final transmission. Because of the low number of transmissions received throughout deployment, battery failure also was unlikely for both sharks. This was further supported by the quality of transmissions not declining over time, which suggested that battery power was sufficient to transmit multiple messages on surfacing. In addition, temperature data for shark 55617 was received until January 2018, which indicated the tag was still trying to transmit to the satellite array.

The most likely cause of tag failure in this study for both sharks was biofouling of the saltwater switch and/or aerial. When shark 55617 was recaptured, both the tag body and aerial were heavily fouled which could explain why both tags ceased transmissions at a similar time if shark 55620 had similar growth on its tag. Hays et al. (2007) reported that battery exhaustion of tags deployed on leatherback turtles (*Dermochelys coriacea*), olive ridley turtles (*Lepidochelys olivacea*) and basking sharks (*Cetorhinus maximus*) was rarely the cause of tag failure. Rather, it was more likely from failure of the saltwater switch due to the accumulation of biofouling organisms. Dicken et al.

(2011) reported barnacles, hydroids, bivalves, polychaetes, algae, ascidians and sponges fouling external surfaces of dart tags of recaptured raggedtooth sharks (*Carcharias taurus*) along the eastern coast of South Africa. Similar organisms have also been reported on Rototags attached to the dorsal fins of blacktip reef sharks (*Carcharhinus melanopterus*), dusky sharks (*Carcharhinus obscurus*) and sandbar sharks (*Carcharhinus plumbeus*) (Heupel et al., 1998), indicating that biofouling was a factor not just limited to this study or type of tag. Heavy biofouling may also lead to eventual aerial breakage hindering the tags ability to transmit. Unfortunately, the composition of fouling species could not be determined in this study. However, the accumulation of fouling species is generally greater in shallower, coastal waters where nutrient availability and species diversity are higher than offshore oceanic environments (Dicken et al., 2011).

On recapture, it was also discovered that tag 55617 was in the process of detaching from the shark's fin and was lying perpendicular to its original position. This would have contributed to signal loss as the aerial would no longer be able to break the surface for transmission. However, when this occurred could not be determined. Satellite tags on the dorsal fins of white sharks have been shown to take between at least 2.2–3.7 years to detach (Nasby-Lucas & Domeier, 2020). Although the fin had healed where damage had occurred from the movement of the tag, slight deformation and possible necrosis and overgrowth of the surrounding fin tissue was evident. Permanent structural fin damage has been reported in white sharks (*Carcharodon carcharias*) where SPOT tag deployment exceeded 24 months before it detached from the fin, and in juveniles and sub-adults where the fin is still rapidly growing (Jewell et al., 2011; Nasby-Lucas & Domeier, 2020). However, in both studies there seemed to be no adverse effects on the movement efficiency, behaviour and long-term survival of tagged individuals. The fin damage identified in shark 55617 suggests that alternative tagging systems could be explored. Pop-up satellite archival tags (PSAT's) provide such an alternative as they are either anchored to the dorsal musculature like a dart tag, or secured to the first dorsal fin through a single hole. However, geolocation estimates from these tags are based on ambient light-level irradiance, with the level of light attenuation determining the accuracy of position estimates (Carlson et al., 2010; Musyl et al., 2011). Although PSAT's have been previously deployed on white sharks in New Zealand with great success (Duffy et al., 2012; Francis et al., 2015a), other studies have reported poor quality light level data due to the higher turbidity found in coastal zones (Carlson et al.,

2010). Therefore, these tags would need to be tested in future studies if considered for use on other species in New Zealand waters.

2.4.2 Geographic Movements

Time until first transmission in sharks 55617 and 55620 was 38.64 and 11.43 days respectively. This could be indicative of a convalescence period following release, which is consistent among large pelagic fishes with the stress of capture (Campana et al., 2009). Such behaviours have been demonstrated in tiger sharks, which after release, shifted into deeper waters to seek refuge in a more favourable environment before returning to the nearshore environment (Afonso & Hazin, 2014). Such depth-holding behaviour could also result in a temporary cessation of feeding behaviour (Campana et al., 2009). Whilst it cannot be determined if such behaviour occurred in the sharks tagged in this study, it is evident that there was a recovery period (particularly in shark 55617) before transmissions at the surface became regular.

The sum of distances between consecutive vectors attained from SPOT5 tag locations indicated shark 55617 travelled a total minimum straight-line distance of 363.49 km over 156.98 days, and shark 55620 travelled a minimum straight-line distance of 568.45 km over 145.34 days. However, these are likely underestimations of true distances travelled, as the movements between transmission locations remain unknown. Recaptures of bronze whaler sharks tagged with conventional dart tags in South Africa reported a maximum minimum straight-line distance of 1320 km between tagging and recapture locations (Cliff & Dudley, 1992). However, the mean distance travelled in this study was 163 km over a period of 162 days at liberty. Bronze whaler sharks also tagged with conventional tags in southern Australia reported straight-line distances travelled of up to 2315 km on recapture (Rogers et al., 2013). But again, mean distance travelled was 225 ± 490 km over a mean duration of 464 ± 714 days at liberty (Rogers et al., 2013). To more closely align the results of this study to the tag and recapture methods of Cliff and Dudley (1992) and Rogers et al. (2013), the distance between tagging location and the transmission furthest from the tagging location was considered (rather than the entire track calculated from the sum of each vector). This decreased the straight-line distance travelled to 137.84 km for shark 55617, and 255.29 km for shark 55620, and provided more comparable results to these tag and recapture studies. This suggests that the sharks tagged in this study undertake similar movements to those

reported in bronze whaler sharks in South Africa and Australia. Furthermore, this demonstrates how tag and recapture methods using conventional dart tags can greatly underestimate distances travelled, and the importance in attaining multiple consecutive location data points for tracked individuals.

The large-scale movements over 1000's of km reported by conventional tagging studies could represent extreme vectors within bronze whaler populations. Alternatively, these large distances travelled could be a result of the longer duration these individuals were at liberty for before recapture. Four sharks in the study by Rogers et al. (2013) travelled distances greater than 1000 km (1088–2315 km) with time at liberty ranging between 951 and 3979 days. This suggests that if the SPOT5 tags secured to bronze whaler sharks in the current study transmitted locations for longer periods of time, greater distances travelled may have been observed. However, some individuals reported by Rogers et al. (2013) only travelled short distances over extended periods of time. For example, one individual travelled a minimum straight-line distance of only 64 km over 1032 days, while another was recaptured in the same location it was tagged after 1087 days at liberty. Because movements between tag and recapture locations are unknown, sharks may have travelled much larger distances, with the small distance reported being a result of site fidelity or philopatric behaviour.

Residency can be defined as the occupation of a limited area by an individual, with site fidelity referring to the reuse of a previously occupied location by an individual after having left it for a period of time (Jorgensen et al., 2010; Chapman et al., 2015). The sharks in this study exhibited a combination of short and long distance movements, which suggested residency within a restricted area of waters and habitats along the north-eastern coastline of the North Island, New Zealand. Sharks travelled no further than the Poor Knights Islands in the north, and Motiti Island in the south. A distance of approximately 261 km over no more than 2.245° of latitude. Within this home range, a high level of site fidelity was evident by the recapture of shark 55617 at its original tagging location at Panepane point at the entrance to the Tauranga Harbour after 539 days at liberty. In addition, bronze whaler sharks tagged with conventional tags as part of the wider study (see Chapter 3) reported the recapture of a mature female (231 cm FL – upper lobe of tail damaged) from a similar location within the Tauranga Harbour just 49 days after its initial capture. Interestingly, on recapture (6th May, 2017), this shark showed evidence of recent mating with fresh wounds such as teeth rakes across its

dorsal surfaces posterior to the first dorsal fin, and may be indicative of an 18 month rather than a one year gestation period if parturition occurs in late spring–early summer as suggested by Cliff and Dudley (1992). Further investigation into the reproductive biology of this species is required to determine if differences exist between global populations. Another recapture was reported on 22nd January, 2018. Again, this was a mature female (286 cm TL_{flex}) which was re-caught at the same location it was tagged along Papamoa Beach, 365 days after its initial capture. A further recapture was reported of another mature female (287.5 cm TL_{flex}) on 17th February, 2018, 315 days after its initial capture. Both landings of this shark occurred at Panepane Point. These recaptures provide the first report of site fidelity in bronze whaler sharks in New Zealand waters. A summary of recapture data can be found in Appendix 5. Evidence of site fidelity within coastal waters over summer was consistent with previous literature. For example, Drew et al. (2019) reported a seasonal return rate of bronze whaler sharks of 77% to the Gulf St Vincent, South Australia, suggesting a large proportion of the population in this study could have made similar returning movements to habitats within the coastal zone. The return of individuals to particular habitats also indicates navigational capabilities such as using geomagnetic, chemical, hydrodynamic and olfactory cues (Nosal et al., 2016).

Because the distribution of bronze whaler sharks in New Zealand encompasses the entire North Island and upper South Island (Francis, 2012), the restricted distribution, and evidence of site fidelity of sharks tagged in this study indicates there could be several distinct populations within New Zealand waters. Therefore, natal philopatry, whereby individuals of a population return to their natal area of origin to breed (Chapman et al., 2015), may also be a factor driving the seasonal movement patterns in this species. The tendency of individuals to return to their natal site is an additional factor confining species to finer geographic scales despite greater mobility potential, and is particularly true for gravid females returning to nursery areas for parturition (Chapman et al., 2015). Therefore, home range is not always indicative of genetic spread, as natal philopatry can contribute to genetically distinct populations, even when the distance between natal sites is less than the known dispersal potential of individuals (Chapman et al., 2015). However, differences in genetic structure were not found over 2700 km of coastline in bronze whaler sharks between South Africa and Namibia, indicating that this might not be the case for this species (Benavides et al., 2011). More accurate definition of their home range size including northern and southern limits, and

inter-population connectivity would require further investigation using techniques such as genetic analysis, and increasing the size of the electronic tagging program. Analysis of catch and release data from the recreational tagging program would also provide further data to support this.

Although sharks displayed latitudinal restriction and site fidelity in their movements, seasonal migratory behaviour away from inshore areas was evident. Although the term migration can be applied to multiple concepts relating to the movement of an animal, the two most applicable to this study describes that migration can be a to-and-fro movement between regions, following favourable conditions and avoiding those that are unfavourable, and a movement that results in a spatial redistribution of a population (Dingle & Drake, 2007). Furthermore, the spatial extent and time period of migration behaviour typically exceed that of other types of movements (Dingle & Drake, 2007). Migration of a population is often in response to the availability and changing location of resources, and is an important component defining the ontogenetic requirements and ecological niche of a species (Dingle & Drake, 2007). The movements of shark 55617 and 55620 during the winter months were dominated by shifts away from the coastline into and beyond shelf-edge regions. The movement into oceanic waters by shark 55620 was also accompanied by a clear movement north of its autumn locations. This data provides first evidence of a seasonal migration offshore during winter for this species. However, a seasonal return to inshore waters the following summer could not be confirmed due to transmissions ending before a return to inshore habitats could be documented. Therefore, the assumptions on migratory behaviour in this species is indicative only. However, the recapture of shark 55617 at its initial tagging location during late winter, 2018, provides evidence of seasonal inshore–offshore migratory behaviour, and a return to inshore waters earlier than previously expected. Furthermore, because only mature females were tagged in this study, differential migration where movements vary between sex, and juvenile and adult groups could not be determined. Longer-term location data along with a larger more diverse data set is required to determine how movements vary across ontogeny, and if these movements are maintained seasonally, or if this species utilises both inshore and offshore habitats year round. However, the lack of sharks in nearshore waters during winter supports this seasonal influence. Repeat migrations between regions of differing resource availability are also typically found in animals with longer life spans supporting a validity of such behaviour in this species (Dingle & Drake, 2007). Similar movements to those found in

this study have been documented in porbeagle sharks (*Lamna nasus*) where summer movements were also focused in nearshore and shelf habitats, with movements to and off the shelf-edge occurring during late summer to early autumn (Pade et al., 2009). However, the movements reported in porbeagle sharks were substantially larger than those found in the bronze whaler sharks in this study.

It is unknown if this species travels further off shore than the movements exhibited by shark 55620 in this study. In particular, if this species migrates between New Zealand and nearby countries such as Australia. However, genetic structure between New Zealand and Australian populations is yet to be detected, suggesting genetic mixing of migratory individuals (Benavides et al., 2011; Junge et al., 2019). Such trans-Tasman panmixia could be aided by the presence of stepping-stone habitats such as the Lord Howe Rise, providing resources and refuge between the two countries. However, thermal preferences may limit such movements.

Despite both sharks exhibiting an offshore shift during winter, there was considerable variability in the overall movement patterns of each individual. Movement patterns in sharks can be in response to a multitude of factors such as temperature, salinity, dissolved oxygen, tidal cycles, light, ontogenetic stage, sex segregation and prey availability (Schlaff et al., 2014). Unlike mammalian species, social transmission of information such as foraging locations has yet to be identified in sharks (Meyer et al., 2010). Therefore, individuals must learn through exploration of their surrounding environment with behavioural polymorphism being explained by the unique experiences of each individual (Meyer et al., 2010). Intra-specific variability in movement patterns have also been described in tiger sharks, where acoustic tagging identified wide-ranging and irregular movements resulting in low spatial and temporal overlap in habitat use between individuals (Meyer et al., 2009). Intra-specific variability in movements would also be expected across ontogeny, as bronze whaler sharks are known to segregate by different size classes and sex (Smale, 1991; Cliff & Dudley, 1992). However, a greater, more diverse sample size of tagged individuals is required to identify how these movements may differ. Ultimately, the movement patterns and habitat use of individuals will determine their success in finding food and potential mates (Papastamatiou et al., 2010). These factors in turn will determine population structure and their influence on top-down processes within food webs (Papastamatiou et al., 2010; Chapman et al., 2015). The degree of residency and site fidelity identified in this

study implies that bronze whaler sharks play an important top-down predatory role in structuring marine communities within north-eastern waters of the North Island, New Zealand. However, further understanding of their seasonal movements and associated feeding ecology is required to understand how this predatory influence may change across seasons, and in turn, how that may affect inshore and offshore prey assemblages.

2.4.3 Swimming Speed

The validity of speed calculations can be compromised when inaccuracies in location estimates are high (Hays et al., 2001). Therefore, reported swimming speed was only calculated from single vectors between two consecutive location estimates of high quality transmissions (LC 3, 2, or 1) to minimise the calculation of over- or under-estimations of swimming speeds for each shark. Furthermore, we only used vectors where directed movement between locations was suspected. However, the speed of each shark could only be calculated as the minimum swimming speed, as the exact movements between these location estimates could not be accurately determined, and may not have been in a straight line as the vector depicts. The minimum swimming speed calculated for shark 55617 and 55620 was 3.63 km/h and 3.06 km/h respectively. Previously, swimming speeds for bronze whaler sharks have not been directly measured. However, a study by Cliff and Dudley (1992) where live bronze whaler sharks caught in beach protective shark nets along the coast of South Africa were tagged and released, reported a movement of an individual between two beaches 53 km apart in one day. This would equate to a swimming speed of 2.21 km/h over a 24 hour time period. The swimming speeds of sharks in this study exceeded that of Cliff and Dudley (1992), and are likely to more accurately represent the minimum swimming speeds of bronze whaler sharks, as the exact time period between release and recapture in the Cliff and Dudley (1992) study was not specified.

The minimum swimming speeds estimated for bronze whaler sharks in this study were comparable to those reported for similar sized tiger sharks tagged in the Eastern Gulf of Shark Bay (ca. 4 km/h, 270–362 cm TL, n = 5; Heithaus et al., 2007b), and white sharks using coastal waters along south-eastern Australia (3.1 km/h, 180–360 cm TL, n = 6; Bruce et al., 2006). However, these values were slower than those calculated for white sharks during transoceanic migrations. Bonfil et al. (2005), reported a minimum swimming speed of 4.7 km/h in a white shark (~380 cm TL) migrating from South

Africa to Australia, and swimming speeds of 3.7–5.4 km/h were reported for white sharks during oceanic crossings from the Chatham Islands, New Zealand (320–450 cm TL, n = 4; Bonfil et al., 2010), indicating that the swimming speed of species may vary depending on the type of movement behaviour performed. Stiff symmetrical tails, such as those of white sharks, are suited for fast open ocean cruising (Fu et al., 2016), and could explain the faster sustained speeds found in white sharks during transoceanic migrations. Furthermore, the regional endothermy and higher metabolic rate found in lamnid sharks to that of other ectothermic species could also be a contributing factor (Bernal et al., 2001). The influence of environmental factors such as ocean currents on swimming speeds is unknown. Interestingly, swimming speed in white sharks was found to be independent of shark length (Bruce et al., 2006). However, a greater sample size representing different size classes would be required to determine if this is also the case in bronze whaler sharks. Although speeds calculated in this study do not represent the maximum speed attainable by this species, comparison against other species, such as white and tiger sharks, may provide a useful measure in determining the travelling or migratory capabilities when deciphering movement data from tracking or genetic studies.

2.4.4 Temperature

A summary of temperature data confirmed the two bronze whaler sharks in this study experienced a wide range of ambient water temperatures from 12–22°C. However, shark 55617 showed a preference for temperatures between 16–20°C, and shark 55620 between 16–22°C. This is similar to the temperature preference of bronze whaler sharks caught in beach protective shark nets along the Natal coastline, South Africa, where 81% of catches were taken in waters where sea surface temperatures were between 19–21.9°C (Cliff & Dudley, 1992). Narrow temperature preferences have also been identified in other carcharhinid species. Hueter et al. (2018) reported silky sharks (*Carcharhinus falciformis*) spent 75.4–78% of their time between 24–27°C, while dusky sharks, although occupying a wide temperature range between 8.8°C and 32.6°C, spent 70% of their time between 23°C and 30°C (Hoffmayer et al., 2010). Silky sharks occupy tropical waters (Hueter et al., 2018) and dusky sharks warm-temperate to tropical (Hoffmayer et al., 2010), which explains why they reported higher ambient water temperatures compared to the bronze whaler sharks in this study.

Summary data also showed a clear pattern of temporal changes in temperature over time. As the winter months (July–September) approached, both sharks experienced steadily declining ambient water temperatures. At time of tagging, inshore water temperatures were around 20–21°C. Temperatures then declined to as low as 13.8°C during winter (mean = 14.89 ± 0.51°C). However, during winter, shark 55620 spent the majority of this time in water temperatures between 16–18°C. With inshore waters not exceeding 16.2°C during this time, this supports the positional data of shark 55620 in offshore waters where water temperatures are warmer and likely to be more consistent. Fewer transmissions were received from shark 55617 during winter compared to shark 55620. However, the data received showed ambient water temperatures between 14–18°C, which could be a result of remaining closer along the shelf slope rather than utilising oceanic waters as shark 55620 did. Cooler upwelling at the slope edge may have also contributed to the lower temperatures experienced by shark 55617. Furthermore, the more northerly winter movements of shark 55620 than 55617 could have introduced a latitudinal effect on temperatures received between the two sharks.

The small amount of time each shark spent between 12–14°C could be an indication of diving behaviour, although the presence of vertical migration has not yet been studied in this species. Diel vertical migration has been reported in porbeagle sharks tagged in New Zealand waters, and is generally considered to be associated with foraging behaviour (Francis et al., 2015b). However, porbeagle sharks experienced temperatures as low as 4.6°C (typically 8–11°C) while diving deep during the day, compared to 13–17°C in the mixed layer at night. This suggests that if the bronze whaler sharks in this study did perform diving behaviour, they remained within the mixed surface layers above the thermocline. If the bronze whaler sharks were regularly performing dives, you would also expect to see a greater spread of their time across a wider range of 2°C time bins. This was evident in shortfin mako sharks, where oceanic individuals experienced time within a greater range of temperatures (9.1–28.3°C), compared to individuals that were vertically constrained by utilising mostly shallower shelf environments, and spending most of their time within a narrower range of temperatures (Francis et al., 2019). Therefore, rather than regular diving behaviour, it is more likely that the time spent by bronze whaler sharks at cooler temperatures (12–14°C) during winter in this study was due to movements back into inshore areas which were not detected by tag transmissions. Travelling at depth between locations for reasons such as navigational purposes or to utilise sub-surface currents have been suggested as plausible

reasons for diving behaviour (Francis et al., 2015b), and may also explain the small amount of time spent in this temperature range by both sharks.

The movement of sharks 55617 and 55620 to shelf and offshore waters during winter could be in response to a thermal cue as coastal and harbour waters begin to cool from around 21.18 ± 1.45°C in summer, to 14.65 ± 0.49°C in winter (https://envdata.boprc.govt.nz/Data). Because continuous location and temperature data from the SPOT5 tags were not received, it was difficult to determine the exact date and temperature the sharks departed from the coastal region. However, on examination of data retrieved by an inshore surface monitoring buoy, the temperature of coastal waters had decreased to around 15°C by the time both sharks had shifted and transmitted from offshore locations. Water temperatures above 16°C have been shown to be important for the presence of bronze whaler sharks in Anegada Bay, Argentina (Lucifora et al., 2005). Furthermore, bronze whaler sharks tracked with acoustic tags within Gulf St. Vincent, South Australia, showed a strong seasonal pattern in shark presence, with detections and the number of sharks within the gulf rapidly declining during the austral winter (Drew et al., 2019). The lowest number of detections coincided with water temperatures below 15°C during the months May to August (Drew et al., 2019). The results of the present study, as well as those of Lucifora et al. (2005) and Drew et al. (2019), indicate a similar temperature threshold triggering the seasonal movements in this species across its range. Similar movements have also been reported in bull sharks (*Carcharhinus leucas*) where tagged individuals were absent within inshore areas of the Gulf of Mexico during winter (Carlson et al., 2010), and juvenile black tip reef sharks (*Carcharhinus limbatus*) which emigrated from their summer nurseries within Terra Ceia Bay, Florida, in response to a rapid decrease in water temperature (Heupel, 2007). However, the recapture of shark 55617 on 23rd September, 2018, at the entrance to the Tauranga Harbour when water temperatures were 15.4°C, along with the low number of detections during winter in Gulf St. Vincent, South Australia when temperatures were below 15°C, indicates these lower temperatures do not completely exclude this species from coastal environments during winter months. However, it does indicate variability of movements not only between individuals, but also of individuals between years in response to changing ambient temperatures.

Temperature has been considered a major factor behind the large-scale movements seen in species such as sharks (Kohler & Turner, 2001). With the exception of the family

Lamnidae, sharks are ectothermic with their internal body temperature being largely influenced by ambient water temperatures. This in turn influences metabolic and physiological processes such as digestion and growth, making them sensitive to environmental change (Schlaff et al., 2014). For example, cardiac function of sharks is limited in cooler temperatures (Weng et al., 2005; Block et al., 2011). Even in endothermic lamnid species, the conservation of metabolic heat occurs only in the red aerobic swimming muscle, eyes, brain and viscera, with the heart being supplied by blood from the gills at ambient temperature (Bernal et al., 2001). Therefore, in response to cooler waters, sharks can experience bradycardia and a lowered cardiac output (Weng et al., 2005). Therefore, when temperature conditions become unfavourable, many species choose to respond by moving, rather than adapting to the new conditions or risking death (Schlaff et al., 2014). Reproductive benefits of remaining within warmer ambient temperatures is also thought to increase the rate of embryonic development due to the maintenance of higher metabolic rates (Hight & Lowe, 2007). Processes that would of course slow down when core body temperatures decrease in response to lowering ambient temperatures (Bernal et al., 2012). However, being a predatory species, it cannot be excluded that the seasonal movement detected in bronze whaler sharks could be in response to the seasonal movement of prey species rather than being primarily influenced by their physiological or thermoregulatory preferences. It is evident that seasonal movements could be due to a number of factors.

2.4.5 Conclusion

Satellite telemetry provided valuable new information on the movements of mature female bronze whaler sharks between coastal waters and shelf-edge and oceanic environments along north-eastern New Zealand. Prior to this study, the surfacing behaviour of bronze whaler sharks was unknown, and there was uncertainty around the efficacy of using SPOT tags on this species given transmissions only occur when the sharks dorsal fin breaks the surface. The results of this study confirm this technology is effective in studying the movement behaviour of bronze whaler sharks despite a low transmission rate, with a large proportion of transmissions providing high accuracy position estimates. However, due to the damage caused to the dorsal fin of one of the recaptured sharks, it would be beneficial to investigate the validity of PSAT's as an alternative method for tracking sharks in a temperate coastal environment.

Furthermore, the occurrence of diving behaviour could be further investigated by the addition of depth sensors to tags.

Preliminary results on the movement behaviour of bronze whaler sharks indicate residency of tagged individuals within the north-eastern region of the North Island, New Zealand. Furthermore, the recapture of multiple individuals within the wider study suggest strong site fidelity and potential natal philopatry to the region. Such findings suggest bronze whaler sharks play an important top-down predatory role in structuring the food web dynamic in this region. Although a larger data set is required, and over a greater period of time, the findings of this study also indicate seasonal migrations of adult female bronze whaler sharks between inshore and offshore waters. Bronze whaler sharks are typically considered residents of shelf habitats. However, the results of this study indicate that shelf-edge and oceanic habitats could also provide important habitat for this species. The different prey assemblages likely encountered between inshore and offshore environments also suggest that as a top-level predator, bronze whaler sharks could influence both inshore and offshore communities across different times of the year. However, perhaps not surprisingly, it is evident that movements vary between individuals, and the movements of male and juvenile sharks remain unknown. Both sharks showed a similar preference in temperature range, which was indicated to be a driving force behind movements into offshore regions as water temperatures in the coastal environment cooled below 15°C during winter. However, whether this was in response to physiological or thermoregulatory preferences, or following movements of prey species is yet to be determined.

An understanding of the movement behaviour and identification of potentially segregated populations of bronze whaler sharks within New Zealand is important for species management, with potentially different population units requiring regional consideration for conservation recruitment potential. This is particularly so given the growing concern over the status of shark populations globally (Heupel et al., 2015). This study provides the first document of movement behaviour of bronze whaler sharks in New Zealand, as well as contributing valuable knowledge on this species for consideration on a global scale. Although further research is required, this study provides an important stepping-stone towards a greater understanding and more effective management of this species and associated habitats in the future.

Chapter 3

Habitat use and diet composition of bronze whaler sharks (*Carcharhinus brachyurus*) in the Bay of Plenty, New Zealand, using $\delta^{13}C$ and $\delta^{15}N$ stable isotope analysis

3.1 Introduction

Given their apex predatory role within marine ecosystems, the trophic ecology of shark species, and how this influences community structure, has garnered much interest among scientists (Estrada et al., 2003). However, the dietary niches of this diverse and elusive group of marine vertebrates have historically been difficult to study in their natural environment. As a result, the trophic ecology and community dynamics of many large shark species remains unknown, hindering the implementation of effective management strategies for rapidly declining populations (Kim et al., 2012b).

Satellite tracking has previously revealed high-resolution information on the spatial and temporal movement patterns of a number of species. However, the factors driving these movements can often be left to speculation, with information on foraging behaviour linked to these movements typically not specified. Furthermore, the high cost of purchasing and deploying satellite-linked tags often results in low sample sizes, potentially creating bias in data where life stages across ontogeny are not adequately represented. Stomach contents analysis presents the traditional method for understanding the species-specific feeding ecology of sharks (Estrada et al., 2003), and with the use of commercial catch, can garner large sample sizes for analysis. However, without such access, sufficient data sets can be difficult to obtain (Madigan et al., 2012). Previously, assessments of stomach contents in bronze whaler sharks (*Carcharhinus brachyurus*) have identified small pelagic teleosts as a dominant prey source (Cliff & Dudley, 1992; Lucifora et al., 2009; Rogers et al., 2012). Demersal teleosts and invertebrates such as cephalopods have also shown to be an important component of the bronze whaler diet across its range (Smale, 1991; Cliff & Dudley, 1992; Lucifora et al.,

2009; Rogers et al., 2012). Although stomach contents analysis provides information on the relative proportions of prey types (Cortés, 1999), stomach analyses are extremely time consuming and laborious, and provide only a snap shot of what an individual has most recently consumed (Madigan et al., 2012). Furthermore, depending of the stage of digestion, there can often be difficulty in accurately identifying consumed species, limiting resolution of the taxonomic level of prey items found. Therefore, assessments of stomach contents may not fully represent the full range of prey species consumed, which can lead to misinformation and biases in our understanding of trophic interactions within the predator community.

Stable isotope analysis provides an alternative, non-lethal technique to supplement information gained from satellite tracking and stomach contents studies. Stable isotope analyses use biogeochemical tracers to investigate the trophic interactions of species, characterising the assimilated diet of a consumer. Therefore, findings represent the long-term spatial and temporal feeding behaviour of an organism, and can provide greater insight into their trophic ecology and role within marine communities than tracking and stomach contents analysis alone (Estrada et al., 2003). In addition, large sample sizes can be collected with minimal invasion to the animal such as blood samples, feather collection, or muscle biopsies, making this technique a particularly valuable tool for studying endangered species without having to sacrifice the animal (Hussey et al., 2010a). Therefore, it is not surprising that the use of stable isotope analysis has become an increasingly important tool in identifying species' diets, trophic relationships, and patterns of resource acquisition within food webs, and is now a widely accepted method of investigation among ecologists (Boecklen et al., 2011; Phillips et al., 2014).

Isotopes are the different forms of an element that vary in the number of neutrons in their nucleus (Fry, 2006). The isotopes of an element are continuously cycling throughout the biosphere at different rates depending on their mass by way of chemical reactions as energy is transferred throughout systems. Because of their lower mass, lighter isotopes typically react faster than heavier isotopes. This relative partitioning between lighter and heavier isotopes is termed fractionation. Stable isotope analysis takes advantage of the varying natural abundance of these different isotopes, measuring the ratio of the heavier isotope to the lighter isotope of an element compared to a standard. Ratios are expressed in delta notation and are defined in parts per thousand

(‰), indicating the percentage of the heavier isotope present in a sample. The higher the delta value, the higher the percentage of the heavier isotope relative to its standard, and the lower the delta value, the lower the percentage of the heavier isotope relative to its standard (Fry, 2006).

Carbon (C) and nitrogen (N) are the two naturally-occurring elements most commonly used in food web investigations using stable isotopes (Layman et al., 2011). As energy is transferred throughout a food web, isotopic discrimination (or enrichment) occurs, resulting in a change in the ratios of the heavy to light isotopes due to fractionation during the uptake, processing and transformation of biological matter into energy for growth (Post et al., 2007). As a result of these metabolic processes, a consumer's tissues typically become more enriched in the less common, heavier isotope relative to its prey (Kim et al., 2012b). This stepwise difference in delta values between a consumer and its prey is referred to as the trophic discrimination factor (TDF) (often also referred to as the trophic enrichment factor). The isotopic ratio of carbon (C^{13}:C^{12}; reported as $\delta^{13}C$) present within the tissues of a predator varies little with successive trophic transfers (0.39‰, SD = 1.3, n = 107; Post, 2002). Therefore, the similar isotope ratio of a consumer to its prey can be used to identify the ultimate sources of carbon from basal productivity assimilated in a consumer's diet when metabolically active tissues such as muscle and blood were formed, providing a valuable indicator of foraging habitat used (Layman et al., 2007a; Li et al., 2016). The isotopic ratio of nitrogen (N^{15}:N^{14}; reported as $\delta^{15}N$) expresses a notably larger enrichment relative to its diet (3.4‰, SD = 0.98, n = 56; Post, 2002). This assimilation of energy flow through the different pathways that lead to a consumer can also provide a continuous measure of the trophic position of an organism, and be used to estimate food chain length (Post, 2002; Li et al., 2016). Therefore, stable isotopes are based on the conjecture of "you are what you eat – plus a few per mil" (Boecklen et al., 2011). The different response of carbon and nitrogen ratios as energy from primary production is transferred throughout the food web provides a valuable biogeochemical tracer, revealing the relative position of species within an isospace matrix, and associated aspects of trophic structure (Layman et al., 2007b). In addition, the ability to calculate the trophic position of an organism provides a more meaningful interpretation of the data than qualitative analysis of raw values (Layman et al., 2011).

The composition of carbon and nitrogen in primary producers set the isotopic baseline $\delta^{13}C$ and $\delta^{15}N$ for the rest of the food web stemming from this basal tier (Graham et al., 2010). Because these $\delta^{13}C$ and $\delta^{15}N$ in primary producers are dependent primarily on their nutrient source, geographic differences in nutrient cycling are known to cause variation in baseline values over small scales, such as inshore–offshore gradients, and on larger scales, such as latitudinal differences across ocean basins (Graham et al., 2010). For example, Hill et al. (2006) reported a spatial trend in the $\delta^{13}C$ values of suspended particulate matter, with nearshore waters being more enriched than those sampled 10 km offshore, suggesting a shift from a nearshore to pelagic supply of carbon. On a much wider scale, baseline values of $\delta^{13}C$ and $\delta^{15}N$ in pelagic ecosystems within the north-east Pacific Ocean decrease around 2–3‰ between temperate and high latitude environments (Graham et al., 2010). Because an organism assimilates the isotopic composition of their prey source, where baseline carbon values are known, stable isotopes can be used to trace the use of isotopically distinct habitats by studied individuals. If the stable isotope value of an individual is similar to that of production at the base of the food web, it can be identified as a resident, foraging from that particular habitat (Graham et al., 2010). However, if the stable isotope value of the individual differs, it indicates it is deriving its energy from a food web with a distinctly different basal carbon source (Graham et al., 2010). Similarly, it is necessary to understand the spatial variation in the baseline values of $\delta^{15}N$, with comparisons of trophic positions between species with distinct basal values leading to inaccuracies where regional values are not accurately recognised.

It is evident that this complex, but predictable nature of stable isotope cycling within the biosphere can have multiple applications in investigating species' diets. More specifically, the use of stable isotope analysis in shark research has elucidated topics of shark ecology such as trophic position (Speed et al., 2012); seasonal diet switching in mako sharks (*Isurus oxyrinchus*) (MacNeil et al., 2005); foraging behaviour of tiger sharks (*Galeocerdo cuvier*), and how it changes across ontogeny (Salinas-de-León et al., 2019); habitat use and low levels of population mixing of black tip reef sharks (*Carcharhinus melanopterus*) between atoll lagoons (Papastamatiou et al., 2010); dietary resource partitioning in sympatric co-occurring shark species within nursery habitats (Kinney et al., 2011); and quantifying carbon flow from primary producers throughout different feeding guilds within communities (McMahon et al., 2016), and across broad spatial scales (Bird et al., 2018). Furthermore, in conjunction with other

techniques such as stomach contents analysis and acoustic telemetry, stable isotope analysis has confirmed long-term residency and trophic overlap in multiple shark species within reef habitats (Speed et al., 2012), and ontogenetic shifts in habitat use in species such as bull sharks (Werry et al., 2011). It is evident that information gained from stable isotope analyses can have important implications in conservation planning such as marine protected areas, with previous research demonstrating the power of stable isotope analyses, particularly when used to complement tracking and stomach contents studies.

Although the trophic ecology of bronze whaler sharks has been previously examined in other countries such as South Africa, Argentina and Australia, methods used have primarily been the use of stomach contents analysis of sharks caught mostly by commercial and game fisheries, and as catch in beach protection nets (Smale, 1991; Cliff & Dudley, 1992; Lucifora et al., 2009; Rogers et al., 2012). To date, there has only been one report globally of the use of stable isotope analysis to investigate the trophic ecology of bronze whaler sharks (Hussey et al., 2015). However, this study only focused on the trophic position in comparison to other shark species, with no investigation into prey sources and predatory connections into the wider community beyond this predator guild. This chapter presents the first look at the trophic dynamic of bronze whaler sharks compared to the wider coastal community in which it interacts. Furthermore, the use of a Bayesian mixing model provides novel insights into the dietary proportions of potential prey species in New Zealand, for which regional data currently does not exist. Therefore, the main objectives of this chapter are:

1) Using $\delta^{13}C$ and $\delta^{15}N$ stable isotopes, investigate the position of bronze whaler sharks relative to the wider coastal community within the Bay of Plenty
2) Using a Bayesian mixing model, investigate $\delta^{13}C$ and $\delta^{15}N$ stable isotopes as indicators of the most important prey items of bronze whaler sharks

Because bronze whaler sharks are typically found in coastal and shelf environments, we hypothesise that when compared to the wider coastal community, the sharks will have a similar $\delta^{13}C$ value to coastal teleost species, indicating the reliance on a similar coastally-derived carbon source. Furthermore, we expect bronze whaler sharks to have

a higher $\delta^{15}N$ value than all other species sampled, indicating its top predatory status within the local food web. Based on previous findings of stomach contents analysis, we expect coastal pelagic teleosts to contribute the greatest proportion to the diet of the bronze whaler shark when assessed using a Bayesian mixing model. The null hypothesis being, that all potential prey species are of equal importance and contribute the same proportion to the diet of bronze whaler sharks in the region.

3.2 Methods

3.2.1 Field Procedure

3.2.1.1 Study Site

A total of 40 bronze whaler sharks were caught from six locations within the Tauranga coastal region, Bay of Plenty, New Zealand (Figure 3.1; Appendix 6). Sampling occurred during the austral summer between 18th November, 2016 and 21st May, 2017. Locations within the southern Tauranga Harbour included an upper harbour and lower harbour site, and were accessed via boat. Land-based locations included Panepane Point at the southern end of Matakana Island at the harbour entrance, a location east of Mount Maunganui main beach, Papamoa Beach, and Pukehina Beach. Land-based excursions were in collaboration with experienced land-based game fishermen who regularly targeted bronze whaler sharks from the shoreline during summer. Therefore, the timing and location of land-based fishing was determined by their availability and choice of fishing location.

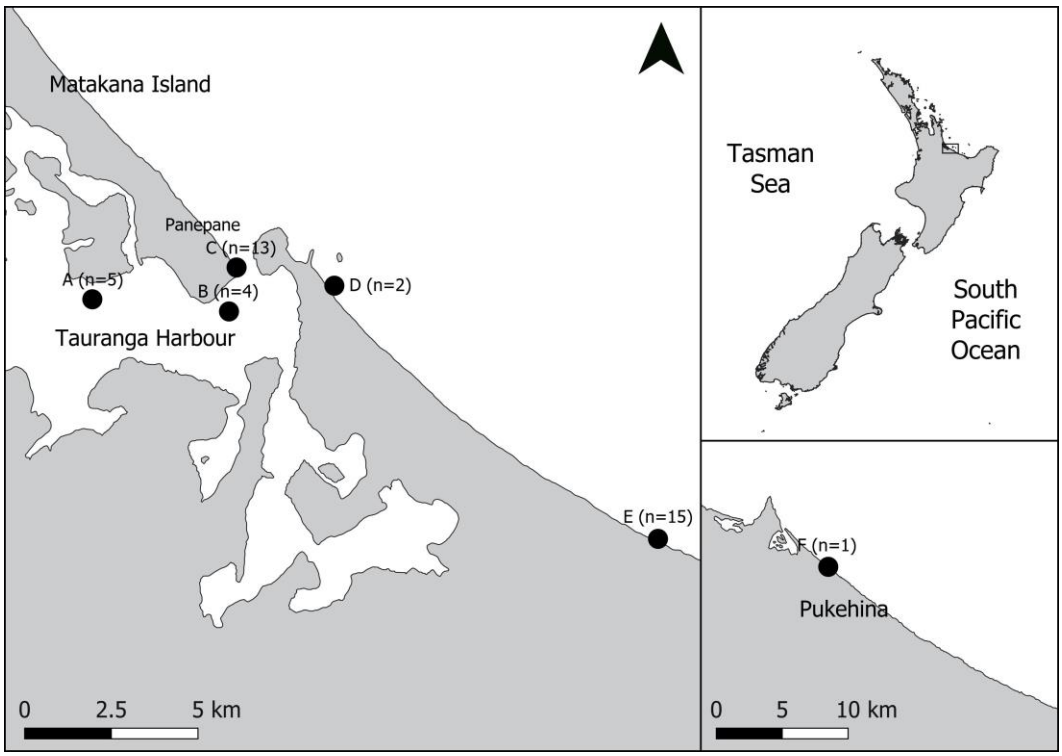

Figure 3.1: Sampling location of 40 bronze whaler sharks (*Carcharhinus brachyurus*) in the Tauranga coastal region, Bay of Plenty, New Zealand. A: Upper Tauranga Harbour; B: Lower Tauranga Harbour; C: Panepane Point; D: Mount Maunganui Beach; E: Papamoa Beach; F: Pukehina Beach. Brackets indicate number of sharks caught at each site. Inset shows New Zealand and Pukehina Beach. Map produced using Quantum GIS (v3.16, Hannover). Spatial data obtained from DIVA-GIS. CRS: WGS84 (EPSG 4326).

The Tauranga Harbour is a large estuary spanning an area of 210 km^2. It is divided into its northern and southern halves by a shallow inter-tidal flat, and protected from the South Pacific Ocean by Matakana Island, a long narrow sand barrier island. The southern end of the harbour hosts New Zealand's largest port in terms of total cargo volume as well as other commercially important industries such as fertiliser and wheat plants. The remaining surrounding areas of the harbour include wastewater treatment facilities, Tauranga City with a growing population currently at 110,338 (worldpopulationreview.com), and established agricultural activities surrounding catchment areas. Outside the harbour, the seaward environment comprises gradually sloping sandy and rocky coastlines, sheltered bays, exposed headlands, and inshore and offshore rocky reefs and islands. Despite the presence of anthropogenic influences, the warm temperate climate and heterogeneity of habitats of the region supports a diversity of temperate and subtropical species throughout various times of the year, including numerous shark species. Commercial and recreational fisheries are also prominent within the harbour and seaward areas of the region. However, there is evidence of biodiversity decline with assessments identifying a reduction of 34% of seagrass beds

within the harbour due to the effects of sedimentation (Park, 1999), highlighting that the coastal system is not free from anthropogenic pressure. Furthermore, introduced species such as the Mediterranean fan worm (*Sabella spallanzanii*) and Asian paddle crab (*Charybdis japonica*) also threaten biodiversity despite large-scale efforts to control these species at both inshore and offshore habitats.

3.2.1.2 Sample Collection

Bronze whaler sharks were captured either from boat, or land-based from the shoreline using a Triton Beast Master 4/0 Shimano big game trolling reel and Shimano IGFA 15 kg Stroker rod. Types of bait used varied between snapper (*Pagrus auratus*), trevally (*Pseudocaranx dentex*) and kingfish (*Seriola lalandi*) frames, king fish heads, eagle ray (*Myliobatis tenuicaudatus*), and shop-bought bonito (family Scombridae) and blue mackerel (*Scomber australasicus*) depending on availability. Boat based fishing also included the use of a 5 kg pilchard (*Sardinops neopilchardus*) and bonito burley bomb. All bait types and fishing methods were successful in attracting sharks and were not considered to cause bias in capture rates. Tackle included Maui SS 16/0 long shank stainless steel circle hooks, with a 600 lb monofilament leader, which had a 0.5 m long double twist at the hook end for extra strength against possible shredding caused by the teeth of the shark. At the opposite end, this leader clipped onto a swivel at the base of a 7.62 m wind-on leader composed of Momoi's Hi-Catch X-Hard 2.05 mm diameter, 400 lb nylon monofilament, which sequentially attached to 100 m of 37 kg Berkley big game nylon overlying 90 lb braid, which comprised the remainder of the line on the reel. All gear was set up professionally at a local fishing outlet, and regularly checked and maintained at a high standard of integrity to avoid any preventable breakages during future captures.

When caught by boat, the vessel was anchored at the edge of the channel in approximately 8–10 m water depth and bait lowered to the sea floor. When a shark was hooked, the anchor was lifted to allow the boat to manoeuvre as the angler brought the shark in alongside parallel to the side of the vessel. The head of the shark was secured toward the bow of the boat using the 2 m long monofilament leader, while the tail was secured by rope around the base of the tail toward the stern. Care was taken to ensure the shark was secured tight enough to minimise movement of the shark, but not causing damage to the jaw where it was still hooked.

Once secured, the sex of the shark was determined by the presence or absence of claspers at the pelvic fins. From the tip of the snout, the pre-caudal (PCL), fork (FL), and total length with the tail in a flexed position so the upper lobe lay along the midline of the body (TL_{flex}) were measured to the nearest 0.5 cm over the curve of the dorsal surface of the body. It is recommended that straight-line lengths are measured rather than measurements over the curve of the body to limit variation caused by differences in girth between individuals (Francis, 2006). However, the design and length of the fishing vessel limited accurate positioning of the tape measure in alignment with the tip of the snout, which would have led to varying accuracy and potential bias in length measurements. Therefore, lengths were measured over the curve of the body so the tape measure could be directly placed at the tip of the snout without a direct line of view. This technique was also used for land-based fishing to ensure standardisation of measurements across the study. Total length with the tail in a natural position (TL_{nat}) was not able to be measured due to boat constraints, and the difficulty in moving sharks on their side on the shore. Flexed total length is preferable due to high measurement error when determining a "natural" tail position (Francis, 2006), but lack of this measure limits comparison with other studies using TL_{nat}. Assumptions of sexual maturity were based on total length measurements. In addition, a fin clip was taken from the posterior margin of the first dorsal fin and stored in 95% ethanol for future genetic analysis, and a tissue biopsy was taken from the right dorsal musculature below the first dorsal fin and kept on ice in 2 ml Cryogenic vials until stored at -20°C until preparation for stable isotope analysis. A conventional Ministry for Primary Industries (MPI) Gamefish stainless steel dart tag was also inserted into the left dorsal musculature at the base of the first dorsal fin for identification purposes and to allow recaptures to be reported to the wider MPI tag and release program. Location, date, and time of capture, landing and release were also recorded. Further information such as mating scars, pigmentation, parasites and temperament of the shark were recorded, and females were noted for possible pregnancy based on the size of their abdomen. However, this could not be accurately determined through just visual observation, with an ultrasound or dissection being required to attain confirmation, but were unable to be performed in this study. Once the sampling procedure was complete, the hook was cut with bolt cutters at the same time the tail rope was removed and the shark was released alive. During release, the shark's body was supported to ensure it was able to swim away without assistance before all contact was removed. The condition of the shark on release was

assessed on a continuum from 0–5, with 0 representing death and 5 indicating that the shark swam away strongly.

Land-based fishing adopted the same methodology described above but with some variation. Baits were either thrown from the shore into the shallows, or paddled to behind the surf break using a kayak. Furthermore, tackle included a 10 m long leader rather than 2 m, to allow the fishermen to safely guide the sharks into the shoreline where it could be temporarily removed from the water so the sampling procedure could be performed. Because the shark was beached, it was positioned on its ventral surface when length measurements were taken and where possible, the hook was completely removed rather than being cut prior to release. Angling times varied depending on tidal conditions, bathymetry, and how the shark responded to capture. However, the sampling procedure took no longer than 21 minutes when sampling by boat, and 11 minutes when land-based.

3.2.1.3 Additional Species Collection

In addition to bronze whaler sharks, tissue samples were taken from coastal teleost, mussel and algal species, along with two pelagic teleost species. To assist in constructing a more dynamic food web, data from previous stable isotope analysis of sponges, and species from within the Tauranga Harbour inter-tidal system were incorporated into analysis.

Coastal teleosts sampled included snapper, kingfish, kahawai (*Arripis trutta*), tarakihi (*Nemadactylus macropterus*) and piper (*Hyporhamphus ihi*). All species had been caught between 5th January and 3rd September, 2017, from various locations within the Tauranga coastal region by local fishermen, and muscle tissue collected from the filleted frames. Detail on capture location, date and FL of each sampled fish can be found in Appendix 7. Because frames were discards from fishermen, animal ethics permission was not required for this collection. Species were selected based on previous knowledge from stomach contents analysis, the literature, and what was available from fishermen, and were considered potential prey species of bronze whaler sharks when in coastal waters.

A total of 70 green-lipped mussels (*Perna canaliculus*) were sampled from four

locations within the Tauranga Harbour and seaward coastal locations (Figure 3.2). Four replicates were collected from each site between the months of December 2016 and May 2017 (Appendix 8). Mussels were collected by snorkel and accessed from the shore. Rather than using the whole organism, the adductor muscle was collected to prevent bias caused by the presence of stomach contents. Mussels were collected under the Ministry for Primary Industries permit SP560 for collection of shellfish. This collection was to provide an isotopic baseline for the coastal food web as they are primary consumers, filter feeding plankton from the water column which could not be sampled directly.

In addition to mussels, macroalgae species were collected to further characterise basal carbon sources of the coastal food web. Kelp (*Ecklonia radiata*) was collected from two locations inside the Tauranga Harbour and outer coastal region between 8th and 14th September 2017 (Figure 3.2; Appendix 9). Lateral fronds were removed from the central lamina and cleaned to remove any sediment and epibiota. Seagrass (*Zostera marina*) was collected from two locations within the Tauranga Harbour on 26th August, 2017. (Figure 3.2; Appendix 9). Roots and rhizomes were removed, so only the leaves were used for analysis. As with the kelp, samples of seagrass were cleaned of sediment and epibiota to prevent bias in analysis.

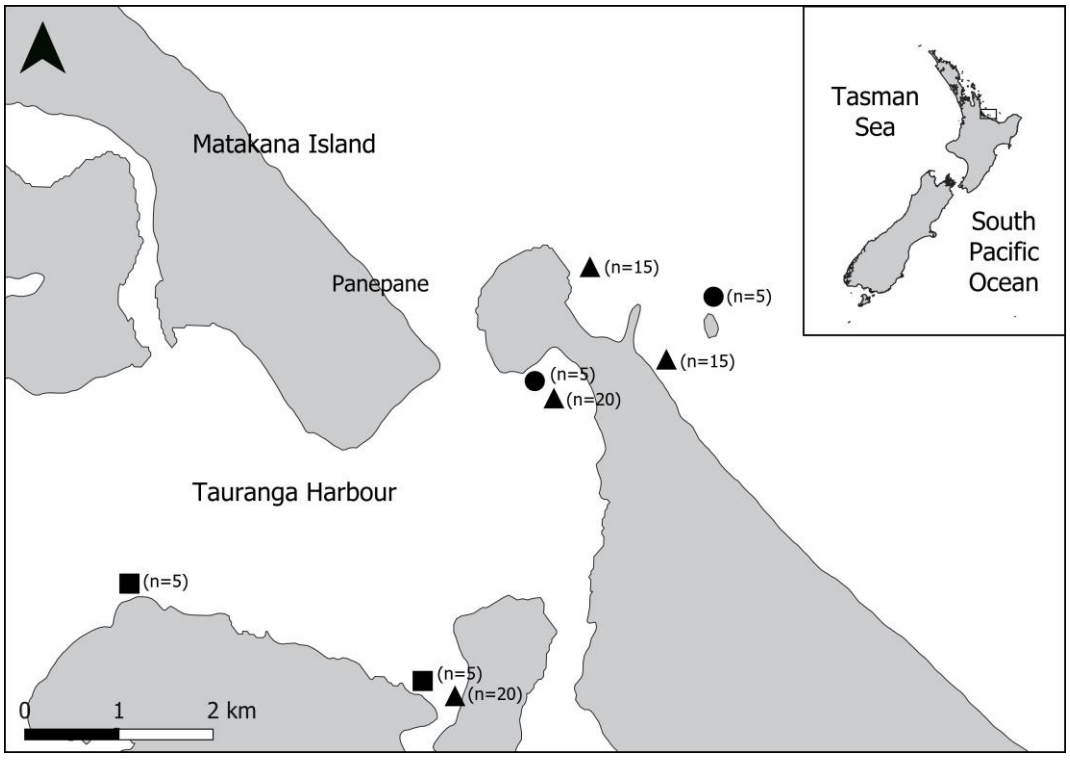

Figure 3.2: Collection locations of green-lipped mussels (*Perna canaliculus*) ▲, kelp (*Ecklonia radiata*) ●, and seagrass (*Zostera marina*) ■, from the Tauranga coastal region, Bay of Plenty, New Zealand, for stable isotope analysis. Inset shows New Zealand. Map produced using Quantum GIS (v3.16, Hannover). Spatial data obtained from DIVA-GIS. CRS: WGS84 (EPSG 4326).

Pelagic teleosts jack mackerel (*Trachurus declivis*) and blue mackerel were supplied by PELCO commercial fisheries. Fish were caught between Waihi and Tuhua (Mayor) Island in the Bay of Plenty region and sampled fresh at the plant before packaging on 11th November, 2020. A block of muscle tissue was excised from the dorsal musculature below the first dorsal fin. Due to time constraints, the length of these fish were not measured but estimated to be around 35–40 cm FL (Appendix 10). Again, because samples were collected from fisheries catch, separate animal ethics permits were not required. These species were collected to provide a pelagic signature for potential prey sources when bronze whaler sharks were utilising offshore habitats. All fish, mussel and algal samples were frozen at -20°C until preparation for stable isotope analysis.

Supporting data was obtained from Huteau (2015) and provided $\delta^{13}C$ and $\delta^{15}N$ values for mud whelk (*Cominella glandiformis*), mud snails (*Amphibola crenata*), cockle (*Austrovenus stutchburyi*), oysters (*Magallana gigas*), sea lettuce (*Ulva lactuca*), mangroves (*Avicennia marina var. australasica*), seagrass, and surface sediment collected from estuarine areas within the Bay of Plenty (Appendix 11). $\delta^{13}C$ and $\delta^{15}N$ values for sponges (*Stellatta crater*) collected from Motunau (Plate) Island, an offshore location, were supplied by McCormack (2021) (unpublished data; Appendix 12).

3.2.2 Lab Procedure

3.2.2.1 Urea Removal

Elasmobranchs are unique among aquatic vertebrates in their adaptations to osmoregulate in a saline environment (Hamlett, 1999). In addition to sodium (Na^+) and chloride (Cl^-), the retention of high levels of urea ($CO(NH_2)_2$) and trimethyl amine oxide (TMAO; C_3H_9NO) in their tissues is used to generate the osmotic and hydraulic pressure gradients required to regulate extracellular body fluids against the surrounding environment (Hamlett, 1999; Fisk et al., 2002; Li et al., 2016). However, because urea is depleted in $\delta^{15}N$, it has been reported to artificially lower $\delta^{15}N$ values in shark tissues, creating uncertainty in isotope measurements and interpretation of ecological data (Li et al., 2016). Furthermore, intra- and inter-specific variation in the level of retained nitrogenous compounds exists due to variable life histories and ambient salinity between individuals and species (Li et al., 2016). Because of this, mathematical correction is not advised as variation in individual paired differences following urea

extraction have previously been reported (Kim & Koch, 2012). As a result, it is recommended that urea is removed from tissue samples prior to stable isotope analysis (Kim & Koch, 2012).

Urea was removed from bronze whaler shark tissue samples using methods described by Kim and Koch (2012), as water rinsing has been shown to be more effective at removing urea than the chemical alternative chloroform/methanol (Li et al., 2016). Each tissue sample was defrosted and placed in an individual 15 ml CELLSTAR® Greiner Bio-One tube filled with 10 ml of deionised water (DIW) and supported in a test tube rack. Each tube was coded with its corresponding sample code to ensure accurate tracing of each sample during processing. Any skin still remaining on the tissue sample from collection was removed at this point so only muscle tissue was being used during processing and analysis. Tube lids were then secured and the rack of samples placed in a sonicating machine with approximately 9 cm depth of cold tap water. Samples were then sonicated for 15 minutes, during which a second set of clean tubes were prepared and coded. After 15 minutes, the DIW from each sample tube was decanted. The bulk of the water from each sample was poured into a waste water beaker, with the remainder of the liquid being filtered using Whatman™ Grade 4 Qualitative Cellulose filter paper (pore size: 20–25 µm) to prevent the loss of any sample tissue. Once fully decanted, the entire process was repeated for a second and third time using clean tubes and fresh DIW each repetition, for a total of 3 x 15 minutes of sonification.

3.2.2.2 Sample Processing

Following urea removal, shark samples were placed in individually coded aluminium pie dishes and dried in an oven at 45°C for at least 24 hours. Because some dried tissue samples were small, they were hand ground until resembling a fine homogenous powder using mortar and pestle. Powdered tissue samples were stored in coded Greiner 2 ml Cryogenic vials until all samples were ready to be weighed. Samples were then transferred into tiered tin capsules (8 × 5 mm) to a weight of approximately 2.5 mg using Sartorius five decimal place balance scales. Once the correct weight was reached, the tissue powder was enclosed within the capsules by pressing into a spherical shape and stored in numbered trays ready for analysis. Marine teleost, mussel and algal samples were prepared in the same manner. However, urea removal was not necessary

for these species, as they do not retain high levels of metabolic waste products for osmoregulatory purposes as elasmobranchs do. Furthermore, some fish species took longer to dry in the oven due to a higher oil content in their tissues. Because the samples from these additional species were larger, samples were ground using a Retsch MM400 ball mill grinder at a frequency of 27.5 oscillations per second for 1 minute each sample. The ground tissue powder was again transferred into 2 ml vials for storage before being weighed out into tin capsules (2.5 mg) for analysis. All grinding equipment and tools were cleaned between grinding and preparing each tin capsule to avoid cross contamination of samples.

Samples were analysed using a Dumas elemental analyser (Europa Scientific ANCA-SL) interfaced to an isotope mass spectrometer (Europa Scientific 20-20 Stable Isotope Analyser) (Sercon Ltd, Cheshire, UK) at the University of Waikato Stable Isotope Unit. Stable isotopes of a sample are measured against a laboratory standard and are presented as delta notation (δ) expressed in parts per mille (‰) using the equation,

$$\delta^{h}X = [(R_{sample}/R_{standard}) - 1] \times 1000,$$

where X is the element, h is the mass number of the heavier isotope, R_{sample} is the ratio of heavy to light isotope ($^{13}C/^{12}C$ or $^{15}N/^{14}N$), and $R_{standard}$ refers to the ratio of the standard. (Kim & Koch, 2012; Shaw et al., 2016). The resulting values represent the difference between the sample and the associated standard rather than a value of the absolute abundance of that particular isotope. The standard reference material for carbon was sucrose with $\delta^{13}C$ of -10.80‰ (from CSIRO, Canberra, Australia), which had been calibrated relative to the Pee Dee Belemnite (PDB) Marine Carbonate Standard. Because PDB has a $^{13}C/^{12}C$ ratio greater than the majority of all other carbon based substances, it was allocated a $\delta^{13}C$ value of zero. As a result, naturally-occurring samples give results with negative delta values due to their lower ratio of carbon isotopes compared to the standard. The laboratory standard for nitrogen was leucine, which has a delta value of 1.00 and was calibrated against atmospheric nitrogen. During analysis, every 10–12 samples were run by the reference materials sucrose ($\delta^{13}C$, -10.80‰) and urea ($\delta^{15}N$, -0.499‰) as a control and provide a within-run instrument precision accuracy of ± 0.5‰ for carbon and ± 1‰ for nitrogen. All C:N ratios were calculated using the units of atom percent.

3.2.3 Analysis

3.2.3.1 Population Dynamics

A histogram of TL_{flex} with 10 cm size bins ranging from 230–310 cm was constructed using females only due to the small number of males sampled during the study. Furthermore, males mature at a shorter length to females and thus could not be directly compared. The length of five female sharks were either estimated or not measured due to time constraints in the field. Therefore, these individuals were removed for length analyses leaving a sample size of 33 females. A one-way analysis of variance analysis (ANOVA) was performed to test if total length varied by month of capture. Data primarily met the assumptions of normal distribution (confirmed by a kurtosis and skewness test for normality) and independence of data, but did not meet the assumption of equal replication. Mindful of unavoidable biases, the ANOVA was constructed to be as robust and conservative as possible. Therefore, data was rationalised to be grouped into the nearest month so that equal replicates (n = 5) of each time block were incorporated (Appendix 13). A one-way ANOVA was also performed to test the effect of location on length. So the ANOVA could be constructed with equal replication, length data was randomly selected where there were at least four replicate measurements. As a result, Mount Beach was removed from analysis. Pukehina Beach was also not included, as a length measurement for this shark was not provided (Appendix 14). For both analyses, significance was indicated by a p value <0.05.

3.2.3.2 Stable Isotope Analysis

3.2.3.2.1 Lipids

Compared to compounds such as proteins and carbohydrates, lipids are typically more depleted in $\delta^{13}C$, thus producing more negative $\delta^{13}C$ values for samples containing a high lipid content (McCutchan et al., 2003; Post et al., 2007; Hussey et al., 2012a). Lipid content of tissues can also vary considerably between individuals and species (Post et al., 2007). Lipids were not chemically extracted prior to processing as this can subsequently cause a small but significant level of fractionation of $\delta^{15}N$ (Post et al., 2007), and has been shown to increase $\delta^{15}N$ values by *c.* 0.5‰ in sand tiger (*Carcharias taurus*) and lemon (*Negaprion brevirostris*) sharks (Hussey et al., 2010a). A strong relationship exists between the carbon-to-nitrogen (C:N) ratio of a sample and its lipid content, providing a reliable indicator of the lipid concentration across various taxa. As

an alternative to chemical extraction, the effect of lipids on $\delta^{13}C$ values was tested post hoc, with C:N ratios >3.5 indicating that lipids were influencing the results of some samples (Post et al., 2007; Hussey et al., 2012a). To normalise each sample for the effects of lipid content, all $\delta^{13}C$ values were mathematically corrected using the formula $\delta^{13}C_{normalised} = \delta^{13}C_{untreated} - 3.32 + 0.99 \times C:N$ (Post et al., 2007) to standardise data across taxa and minimise lipid-induced bias. Although animals, sponges lack true tissues such as muscle, fat and nervous tissue (Urry et al., 2018). Therefore, sponges were excluded when mathematical correction was performed to prevent an artificial correction value being calculated. Plants and surface sediment were also excluded from correction for this reason. To identify the effects of lipid normalisation on $\delta^{13}C$ values, paired t-tests were performed to test the significance of any changes in values following correction (Appendix 15).

3.2.3.2.2 $\delta^{13}C$ and $\delta^{15}N$

Size-based $\delta^{13}C$ and $\delta^{15}N$ profiles were plotted for bronze whaler sharks to identify any trophic shifts across ontogeny. A biplot showing mean isotopic signatures $\delta^{13}C$ and $\delta^{15}N$ for all species sampled was constructed using the ggplot2 package (Wickham H, 2016) and base **R** 3.5.0 (**R Core** Team, 2018) run through Rstudio (RStudio Team, 2020).

3.2.3.2.3 Trophic Discrimination Factor (TDF)

Stable isotope ratios of consumers are typically more enriched than their diet (Post, 2002; McCutchan et al., 2003). However, the degree of trophic shift between consumers and their prey can vary considerably due to metabolic fractionation and assimilation processes differing between species, tissue types and with diet quality (McCutchan et al., 2003; Hussey et al., 2010a). This trophic shift is referred to as the diet-tissue trophic discrimination factor (TDF), and is assigned the symbols $\Delta\delta^{13}C$ and $\Delta\delta^{15}N$ to note the change in $\delta^{13}C$ and $\delta^{15}N$ values between predators and their prey. The utility of ecological studies using stable isotopes are dependent on accurate assumption of TDF values to avoid erroneous interpretation of stable isotope data. In particular, the correct use of $\Delta\delta^{13}C$ and $\Delta\delta^{15}N$ values is a requirement to avoid bias when predicting dietary sources in mixing model analyses, and when estimates of trophic position are calculated (Hussey et al., 2010b). Although TDF values have been well studied for taxa such as birds, mammals, and fish through controlled feeding experiments,

elasmobranch-specific values have been limited due to the difficulty in keeping such species in captivity (Hussey et al., 2010a; Kim et al., 2012a). Surrogate values of $\Delta\delta^{13}C$ 0.39‰ and $\Delta\delta^{15}N$ 3.4‰ reported in a review by Post (2002), have been widely applied throughout the literature assuming constant TDF values across a range of isotopic frameworks (Hussey et al., 2010a). However, such values should be used with caution, as they overlook known variation between taxa, which can result in the misinterpretation of ecological data where generalised values are applied. Because the actual TDF values of bronze whaler sharks have not yet been determined, our data adopted a $\Delta\delta^{13}C$ value of 0.4‰ and $\Delta\delta^{15}N$ value of 2.3‰ based on those calculated for muscle tissue of aquatic poikilotherms (McCutchan et al., 2003), and providing a more accurate estimate than the generally assumed surrogate value of $\Delta\delta^{15}N$ of 3.4‰ and $\Delta\delta^{13}C$ of 0.39‰ suggested by Post (2002).

3.2.3.2.4 MixSIAR Bayesian Mixing Model

Stable isotope mixing models assess the relative contribution of multiple prey species (sources) to the diet of a predator (mixture) when species and tissue specific trophic discrimination factors are accurately applied (Hussey et al., 2010a). Where accurate TDF values are used, there can be greater confidence in the output of diet reconstruction models. This study used the Bayesian mixing model program MixSIAR (stable isotope analysis in R) to evaluate the contribution of potential food sources to the diet of the bronze whaler shark. Seven teleost food sources were used: kahawai, kingfish, piper, snapper, tarakihi, blue mackerel and jack mackerel, with an assumed trophic discrimination factor of +0.4‰ for $\delta^{13}C$ and +2.3‰ for $\delta^{15}N$ (McCutchan et al., 2003). An initial isospace plot indicated that bronze whaler shark values fell within the end members of adjusted prey species confirming that analysis could progress with a mixing model. Because no prior information on diet proportions of sources was available, an uninformative prior was applied indicating all combinations of dietary proportions were equally likely. A long chain length with 100,000 Markov Chain Monte Carlo (MCMC) repetitions was used to estimate the distribution of each variable. A Gelman-Rubin Diagnostic <1.05 and Geweke Diagnostic <5% indicated convergence and true posterior distribution was met (Appendix 16). The Deviance Information Criterion (DIC) value was 9.130363. Model output included a prior and pairs plot which are shown in Appendix 17 and 18 respectively, along with an isospace plot, scaled posterior probabilities plot, and summary statistics table which are presented in the text.

Posterior probabilities of dietary contributions for each source species were normalised so the maximum value for each species was constrained to 1.

3.2.1 Ethics Statement

The work undertaken in this project was approved by the University of Waikato Ethics committee Protocol #974. This research did not involve interaction with threatened or protected species. Furthermore, no animals were sacrificed in the study, and procedures were put in place to ensure replacement, reduction and refinement to minimise any impact on the study animals. As a result, this research was considered to have moderate impact on the study species.

3.3 Results

3.3.1 Population Dynamics

A total of 40 bronze whaler sharks were caught from six locations within the Tauranga coastal region between 18th November, 2016, and 21st May, 2017. Thirty-eight sharks were female, and two males, providing a male to female sex ratio of 1:19 caught within coastal habitats during the sampling period. Females ranged in length from 236–305 cm TL_{flex} (mean ± standard deviation; 283.12 ± 18.24), with 66.67% of females caught being greater than 280 cm in length (Figure 3.3). Previously established length at maturity measurements indicate that females mature between 215–271 cm TL (Walter & Ebert, 1991; Smale, 1991; Lucifora et al., 2005; Drew et al., 2016). Therefore, 88–100% of females sampled were considered to have reached sexual maturity. Males are reported to mature between 200 and 220 cm TL (Smale, 1991; Walter & Ebert, 1991; Lucifora et al., 2005; Drew et al., 2016). The two males caught in this study measured 286 and 293 cm TL_{flex}. Based on this, both males were considered mature, which was further confirmed through complete calcification of their claspers.

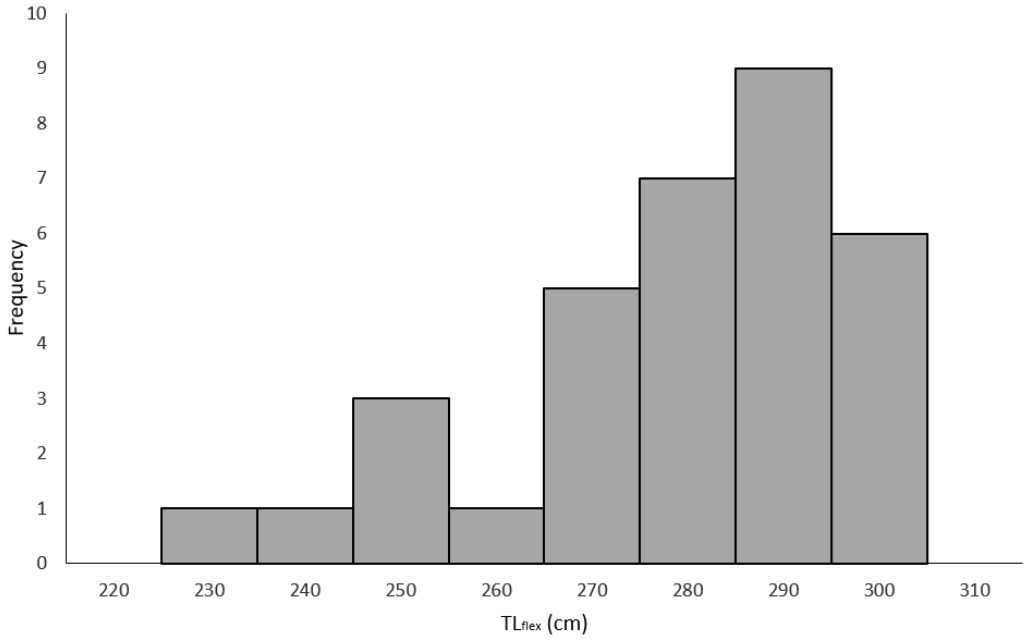

Figure 3.3: Length-frequency histogram of mature female bronze whaler sharks (n = 33) caught between 18th November, 2016, and 21st May, 2017, from coastal habitats within the Bay of Plenty, New Zealand. The length range for each bar begins with the TL_{flex} (cm) value immediately beneath.

One-way ANOVA tests revealed a significant relationship between shark length and month of capture ($p<0.05$; df = 5, 29), with indication that larger sharks were caught during the month of February (Figure 3.4; Appendix 13). However, this result needed to be treated with caution due to the limited sampling effort that was possible during spring and autumn. This created sampling bias preventing our ability to run a balanced analysis. Therefore, n = 5 represents the maximum number of sharks from the least productive time period. The relationship between total length and location was not significant, indicating that the length of sharks was similar, irrespective of location of capture ($p>0.05$; df = 3, 15) (Figure 3.5; Appendix 14).

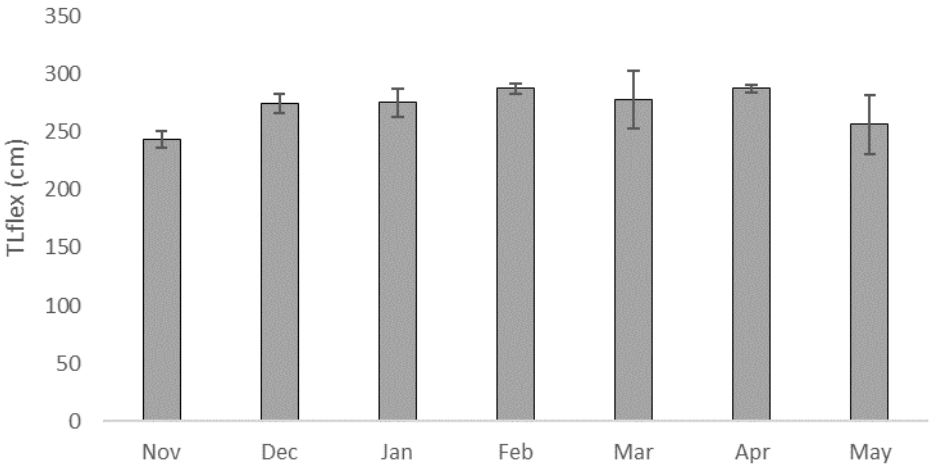

Figure 3.4: Average length (±SE) of bronze whaler sharks (*Carcharhinus brachyurus*) (n = 33) caught monthly between 18th November, 2016, and 21st May, 2017, from coastal habitats within the Bay of Plenty, New Zealand.

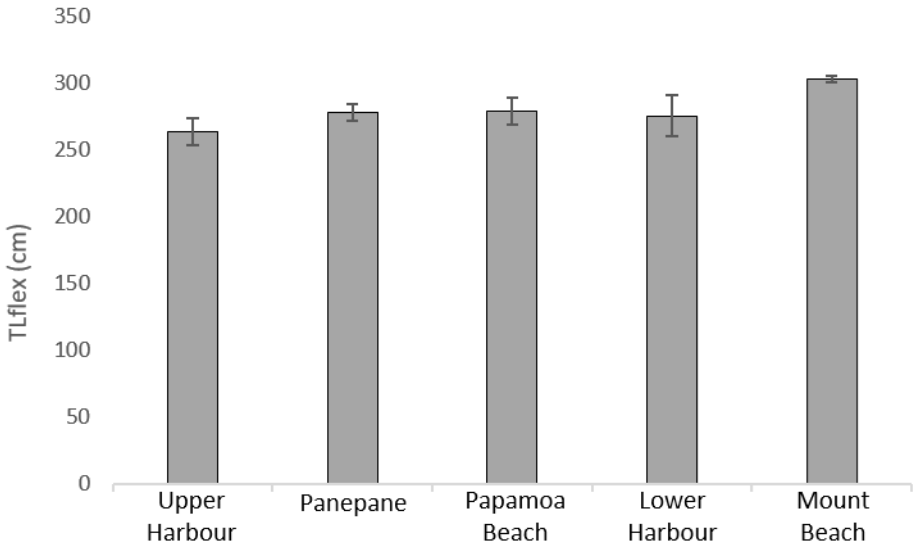

Figure 3.5: Average length (±SE) of bronze whaler sharks (*Carcharhinus brachyurus*) (n = 33) caught from each coastal location between 18th November, 2016, and 21st May, 2017 in the Bay of Plenty, New Zealand.

3.3.2 Stable Isotope Analysis

3.3.2.1 Lipids

The effect lipid treatment had on $\delta^{13}C$ values was variable among species. A paired t-test identified there was no significant difference in $\delta^{13}C$ values following mathematical correction for kingfish, snapper and tarakihi ($p>0.05$). This indicated that lipid content was already low in the tissues of these species. Therefore, the effect of correction was

minimal. However, a significant difference following treatment was identified in bronze whaler sharks, piper, kahawai, jack mackerel, blue mackerel, green-lipped mussels, mud snails, cockles, oysters and mud whelk ($p<0.05$) (for full analyses see Appendix 15). Although the degree of significance was variable among species, it indicated the higher lipid content of these tissues was having an effect on the $\delta^{13}C$ values of untreated samples and lipid extraction or mathematical correction was required.

3.3.2.2 $\delta^{13}C$ and $\delta^{15}N$

The $\delta^{13}C$ values of male and female sharks between 236–305 cm TL_{flex} were highly clustered around a mean of -16.17‰ ± 0.36 (range: -16.90‰ to -14.83‰; n = 40). A significant linear relationship between shark length and $\delta^{13}C$ values was not identified, indicating that all sharks in the sample were feeding on similar prey items within similar habitats ($R^2 = 0.134$) (Figure 3.6a). The limited variability in $\delta^{15}N$ values (mean = 16.62‰ ± 0.45; range: 15.70‰ to 18.42‰; n = 40) also led to the absence of a linear relationship between shark length and $\delta^{15}N$ ($R^2 = 0.0116$) (Figure 3.6b), which indicated that all sharks were feeding at a similar trophic level.

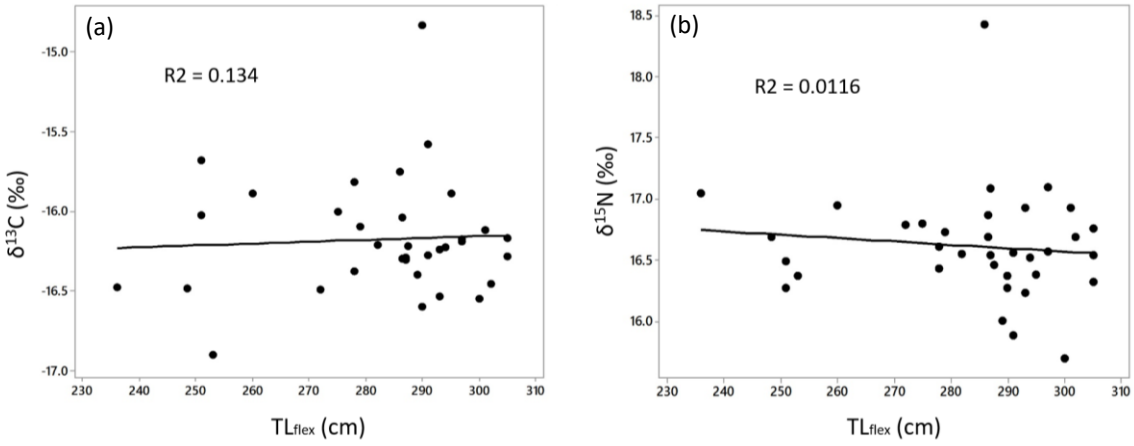

Figure 3.6: Sized-based $\delta^{13}C$ and $\delta^{15}N$ ontogenetic profiles of bronze whaler sharks (*Carcharhinus brachyurus*) fitted with linear regression models (black line). Sharks were caught between 18th November, 2016, and 21st May, 2017, from coastal habitats within the Bay of Plenty, New Zealand.

Overall, 369 samples were taken from 19 species for stable isotope analysis. For all species, average $\delta^{13}C$ values ranged from -26.39‰ to -11.58‰, and average $\delta^{15}N$ values ranged from 5.37‰ to 16.61‰ (Figure 3.7; Table 3.1). Variance in mean $\delta^{13}C$ and $\delta^{15}N$ values also differed within species. For example, the variance of $\delta^{13}C$ in piper and

kingfish was greater than the variance found in $\delta^{15}N$, indicating a non-linear interaction of $\delta^{13}C$ and $\delta^{15}N$ across the delta space matrix in these species. Inter-specific variation was also evident indicating varying feeding strategies between species (Shaw et al., 2016). Trophic positions were evident in the upper levels of the food web.

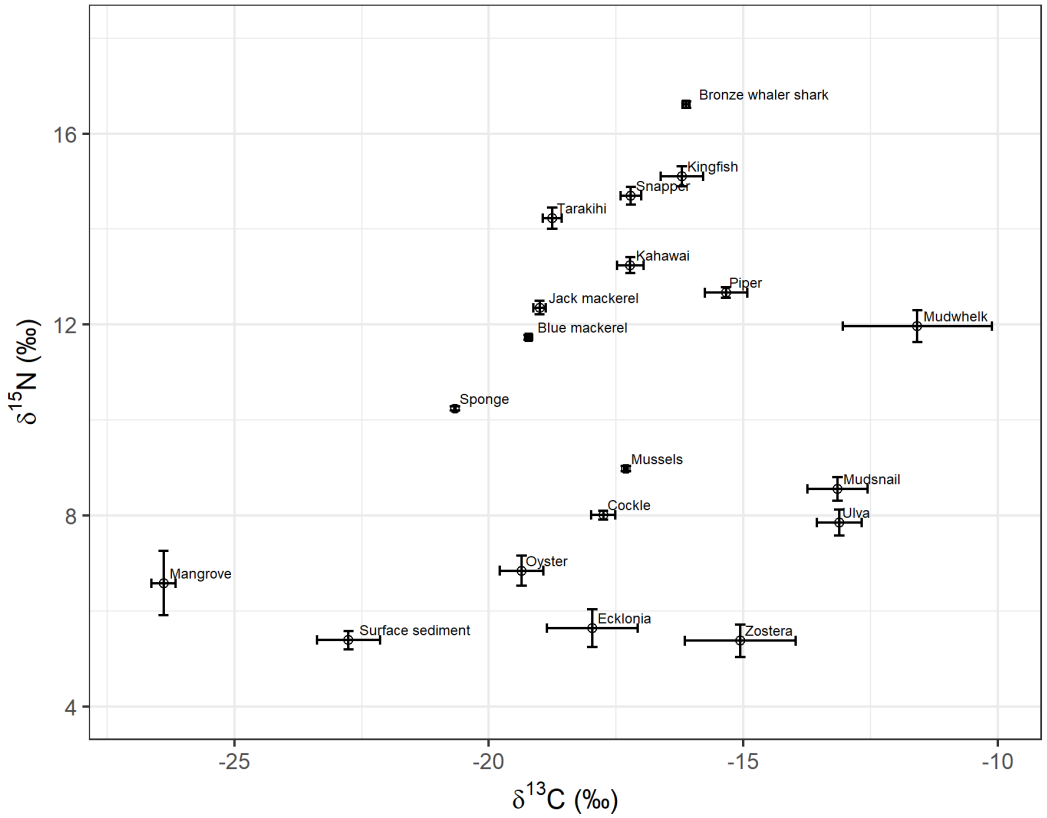

Figure 3.7: Stable isotope values $\delta^{13}C$ and $\delta^{15}N$ (mean ± SE) for bronze whaler sharks, and teleosts, invertebrates and primary producers belonging in the communities within the Bay of Plenty, New Zealand.

Bronze whaler sharks were the most enriched in $\delta^{15}N$ indicating their apex predatory status within the predator community. Based on a TDF of 2.3‰ for $\delta^{15}N$, teleost species presented potential prey items to the diet of the sharks. Among teleosts, blue mackerel and jack mackerel were the least enriched, which may be a reflection of their pelagic existence and planktonic prey sources. However, stable isotope values identify potential prey sources for teleost species had been missed in this species collection. *Zostera marina*, microphytobenthos on surface sediment and *Ecklonia radiata* were the least enriched in $\delta^{15}N$ (means 5.37‰, 5.39‰, and 5.64‰ respectively) and most likely represented basal production within the coastal communities.

Table 3.1: Stable isotope values $\delta^{13}C$ and $\delta^{15}N$ (mean ± SD) for bronze whaler sharks, and teleost, invertebrate and basal species belonging to the predator community within Bay of Plenty, New Zealand. Sample size (n).

Species	Scientific name	n	$\delta^{13}C$	$\delta^{15}N$
Bronze whaler shark	*Carcharhinus brachyurus*	40	-16.12 ± 0.37*	16.61 ± 0.42
Snapper	*Pagrus auratus*	10	-17.21 ± 0.65*	14.70 ± 0.59
Kingfish	*Seriola lalandi*	9	-16.21 ± 1.26*	15.11 ± 0.63
Kahawai	*Arripis trutta*	20	-17.22 ± 1.16*	13.24 ± 0.74
Tarakihi	*Nemadactylus macropterus*	9	-18.76 ± 0.55*	14.22 ± 0.66
Piper	*Hyporhamphus ihi*	5	-15.35 ± 0.93*	12.67 ± 0.25
Jack mackerel	*Trachurus declivis*	15	-19.00 ± 0.46*	12.35 ± 0.54
Blue mackerel	*Scomber australasicus*	15	-19.22 ± 0.22*	11.73 ± 0.18
Green lipped mussel	*Perna canaliculus*	70	-17.31 ± 0.27*	8.98 ± 0.50
Kelp	*Ecklonia radiata*	10	-17.97 ± 2.82	5.64 ± 1.25
Seagrass**	*Zostera marina*	10	-15.06 ± 6.07	5.37 ± 1.90
Mud whelk***	*Cominella glandiformis*	3	-11.58 ± 2.53*	11.97 ± 0.58
Mud snails***	*Amphibola crenata*	22	-13.15 ± 2.77*	8.56 ± 1.17
Cockles***	*Austrovenus stutchburyi*	13	-17.75 ± 0.85*	8.01 ± 0.33
Oysters***	*Magallana gigas*	12	-19.35 ± 1.47*	6.84 ± 1.09
Sea lettuce***	*Ulva lactuca*	14	-13.12 ± 1.64	7.86 ± 1.02
Mangroves***	*Avicennia marina var. australasica*	20	-26.39 ± 1.05	6.58 ± 3.01
Microphytobenthos***		45	-22.76 ± 4.15	5.39 ± 1.29
Sponges****	*Stellatta crater*	6	-20.67 ± 0.03	10.24 ± 0.11

*Mathematically corrected for lipid content
**Combined with data obtained from Huteau (2015)
***Obtained from Huteau (2015)
****Obtained from McCormack (2021)

3.3.2.3 Bayesian Mixing Model

The biplot showing $\delta^{13}C$ and $\delta^{15}N$ values of the predator community identified teleost species as plausible prey items of bronze whaler sharks for use in Bayesian mixing model analysis conducted with the R package MixSIAR (Stock et al., 2018). An initial dual isotope biplot applying a trophic discrimination factor of +0.4‰ for $\delta^{13}C$ and +2.3‰ for $\delta^{15}N$ to prey species indicated that values for the consumer, bronze whaler sharks, fell within the end members of adjusted prey species (Figure 3.8). This confirmed that the mixing model was likely to converge.

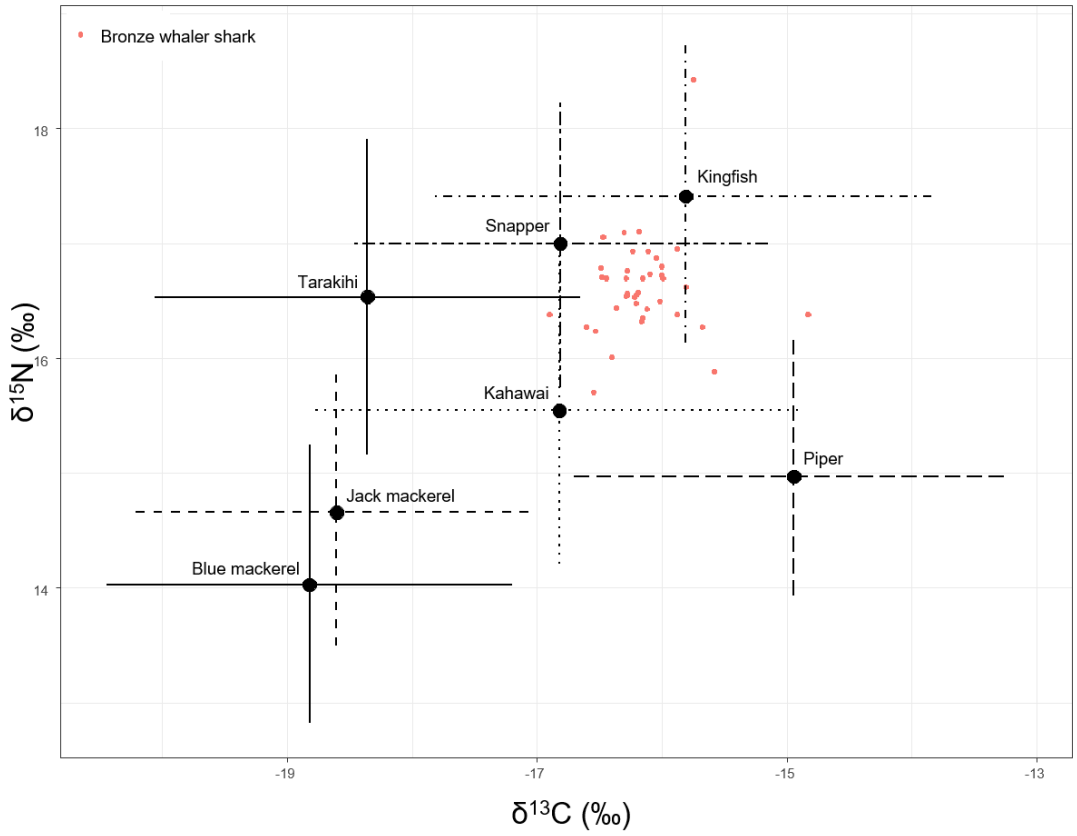

Figure 3.8: Comparison of $\delta^{13}C$ and $\delta^{15}N$ values of bronze whaler sharks (*Carcharhinus brachyurus*) (individuals represented as pink dots), and their potential teleost prey sources (means with error bars of 1 SD) from the Bay of Plenty, New Zealand. Potential prey sources have been adjusted using a trophic discrimination factor of +0.4‰ for $\delta^{13}C$ and +2.3‰ for $\delta^{15}N$.

The Bayesian mixing model determined the relative contributions of teleost species kingfish, snapper, tarakihi, kahawai, piper, jack mackerel and blue mackerel to the diet of bronze whaler sharks. For each source, a probability distribution curve of isotopically feasible contributions to the predator diet was produced (Figure 3.9; Table 3.2). Consumption of kingfish accounted for 24.8–69.6% (2.5–97.5 percentiles; mean = 50.7%) of the bronze whaler shark diet, providing the greatest contribution of prey species. Piper was also an important prey source contributing 0.7–25.5% (2.5–97.5 percentiles; mean = 11.5%) to the predator diet. The remainder of the diet was made up of snapper (0.4–44.3%; mean = 13.8%), kahawai (0.3–27.2%; mean = 8.8%), tarakihi (0.3–20.1%; mean = 6.5%), jack mackerel (0.2–15.7%; mean = 4.7%), and blue mackerel (0.1–13.4%; mean = 4.0%).

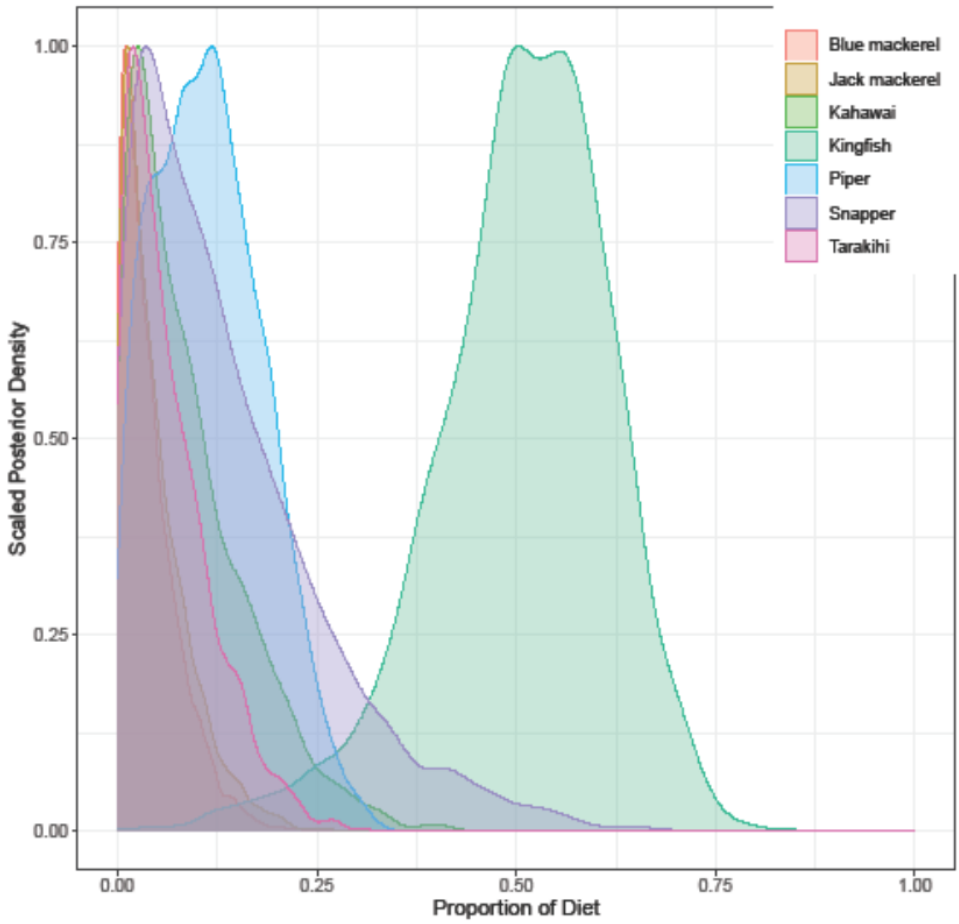

Figure 3.9: Scaled posterior probabilities of the contribution of teleost species to the diet of bronze whaler sharks (*Carcharhinus brachyurus*) caught from coastal habitats within the Bay of Plenty, New Zealand.

Table 3.2: Posterior probabilities of the contribution of teleost species to the diet of bronze whaler sharks (*Carcharhinus brachyurus*) caught from coastal habitats within the Bay of Plenty, New Zealand, estimated from the Bayesian mixing model MixSIAR. Values show mean probability, SD and 2.5–97.5 percentiles for each prey species.

Species	Mean	SD	2.5%	5%	25%	50%	75%	95%	97.50%
Blue mackerel	0.040	0.036	0.001	0.002	0.013	0.031	0.059	0.113	0.134
Jack mackerel	0.047	0.042	0.002	0.003	0.015	0.035	0.068	0.134	0.157
Kahawai	0.088	0.074	0.003	0.005	0.029	0.068	0.127	0.229	0.272
Kingfish	0.507	0.111	0.248	0.308	0.445	0.517	0.583	0.667	0.696
Piper	0.115	0.067	0.007	0.015	0.061	0.111	0.162	0.234	0.255
Snapper	0.138	0.117	0.004	0.009	0.046	0.108	0.197	0.375	0.443
Tarakihi	0.065	0.054	0.003	0.005	0.023	0.051	0.094	0.170	0.201

There was a strong negative correlation between the consumption of snapper and kingfish (-0.80) (Appendix 18). This indicates that if snapper are being consumed at the top of their probability range, then kingfish are likely being consumed at the bottom of theirs. No other correlations of strength in the proportion of prey contributions were identified.

3.4 Discussion

3.4.1 Population Dynamics

Fish length is an important measure when determining life history characteristics such as size at maturity, and the maximum size of a species (Francis, 2006). Based on the total length of female sharks caught in this study, 88–100% were considered mature, while the total length and calcification of claspers confirmed maturity in both males. Therefore, the results and wider discussion of this chapter are only applicable to mature bronze whaler sharks, as juvenile and sub-adult cohorts were not represented. The length range of females was 236–305 cm TL_{flex}, which was within the maximum length (308 cm TL; Drew et al., 2016) reported for this species. Males measured 286 and 293 cm TL_{flex}, which fell within the maximum length recorded for males of 294 cm TL (Walter & Ebert, 1991).

Out of the 40 bronze whaler sharks caught within the Tauranga coastal region, only two were male providing a male to female sex ratio of 1:19. Previous examination by Smale (1991) and Drew et al. (2016) reported uterine male to female sex ratios of 1:1 and 1.15:1 respectively. More recently, a sex ratio of 1:2 was observed in a female beach-cast at Papamoa Beach, Bay of Plenty, New Zealand (pers. obs.). However, this does not explain the difference in numbers of males to females caught during this study. The ratio of 1:19 suggests a behavioural influence with sex segregation being evident in this species (Smale, 1991; Cliff & Dudley, 1992). Therefore, it is possible that the low numbers of males caught was due to their primary utilisation of a different habitat away from coastal environments. Alternatively, males were also present within these inshore habitats, but were not attracted to the baits used during fishing as the females were, making them harder to catch. The use of coastal habitats primarily by females may also indicate a level of philopatry to inshore environments for reproductive behaviour such as parturition.

One-way ANOVA results confirmed that location of capture had no effect on shark length ($p>0.05$). However, month of capture did ($p<0.05$), with a weak but significant effect indicating that larger sharks were caught during the summer month of February. Parturition is thought to occur from October to December (Walter & Ebert, 1991; Cliff & Dudley, 1992; Lucifora et al., 2005). However, the presence of larger females during February might suggest the use of coastal waters for parturition later into the summer

period than previously reported. Information on parturition sites and nursery areas is limited in this species, particularly in New Zealand. Therefore, further research would be required to understand the timing of large, mature females within inshore areas against periods in which parturition occurs. Alternatively, females may utilise warmer, shallower waters for thermoregulatory and metabolic processes favouring embryonic development.

3.4.2 Lipids

Although not all samples had a C:N ratio >3.5, because this study compared species and individuals with variable lipid content, all data were mathematically corrected for lipids to standardise $\delta^{13}C$ values across sampled taxa. The equation used was developed by Post et al. (2007), who evaluated the use of direct chemical extraction and mathematical normalisation when dealing with the effects of lipid concentrations on $\delta^{13}C$ values, and confirmed that mathematical correction was comparable to chemical extraction prior to analysis. Because the level of bias introduced increases as lipid content of a sample increases, post hoc lipid correction had minimal effect on those samples that already contained low levels of lipid concentrations compared to those with a higher lipid content (Post et al., 2007). The difference between $\delta^{13}C$ values pre- and post-lipid correction was not significant for kingfish, snapper or tarakihi. However, it was significant in bronze whaler sharks, piper, kahawai, jack mackerel, blue mackerel, green-lipped mussels, mud snails, cockles, oysters and mud whelk, indicating lipids had an effect on initial results derived from muscle tissue of consumer and potential prey species. Similar effects have been reported by Hussey et al. (2010a) who also reported a significant increase in $\delta^{13}C$ following lipid correction. This indicates the importance of understanding the lipid content of samples for isotope studies, and correcting accordingly to prevent bias in analysis.

3.4.3 $\delta^{13}C$ and $\delta^{15}N$

Sized based $\delta^{13}C$ and $\delta^{15}N$ profiles did not identify the presence of an ontogenetic shift in $\delta^{13}C$ and $\delta^{15}N$ values with increasing size. However, assuming all individuals within the data set were mature adults, juvenile and sub-adult life stages were missing within this data set. If these groups were also included, it is likely that a change in trophic position and feeding habitat with increasing length would have been identified. Such a relationship was found in scalloped hammerheads, which showed a significant increase

in $\delta^{15}N$ values as sharks increased in size (Hussey et al., 2011). However, what can be derived from the data in this study, is that once bronze whaler sharks reach maturity, they typically feed in the same habitats and at a similar trophic level. There was a presence of an outlier, which is to be expected in biological data. This individual was one of the two males caught (286 cm TL_{flex}), with a $\delta^{15}N$ value of 18.42‰. This increased $\delta^{15}N$ could be an indication of diet expansion into larger prey species such as small sharks, or cannibalism, which may have resulted from intra-specific variability in movement patterns or prey preferences experienced by this individual. This could also be attributed to differences in habitat use between male and female sharks, as sex segregation has been identified in this species (Smale, 1991; Cliff & Dudley, 1992). However, a larger, more representative data set for males would be required to substantiate this hypothesis.

3.4.4 Trophic Discrimination Factors

The trophic discrimination factor (TDF) values used in this study for $\Delta\delta^{13}C$ and $\Delta\delta^{15}N$ of muscle tissue were 0.4‰ and 2.3‰ respectively, and were taken from McCutchan et al. (2003). These values were specified for aquatic poikilotherms and were similar to those of $\Delta\delta^{13}C$ 0.9‰ and $\Delta\delta^{15}N$ 2.29‰ reported by Hussey et al. (2010a) who calculated the TDF of sand tiger sharks (*Carcharias taurus*), supporting the estimates of McCutchan et al. (2003) for use for large carnivorous shark species. However, Hussey et al. (2010a) had a small sample size due to the use of sharks in aquaria for testing, along with estimates of TDF values being mathematically modelled rather than directly measured. In comparison, values from McCutchan et al. (2003) were based on a review of published studies on consumers raised on controlled diets, and thus, were favoured over those by Hussey et al. (2010a).

However, these results varied from those of Kim et al. (2012a) and Kim et al. (2012b) who reported larger TDF values ranging from 1.7–3.5‰ for $\Delta\delta^{13}C$, and 3.7–5.5‰ for $\Delta\delta^{15}N$. However, the species used in their feeding experiments was the leopard shark (*Triakis semifasciata*), which is a smaller species (<2 m length) (Kim et al., 2012a), typically occupying a benthic niche feeding on prey items such as bivalves, crabs, cephalopods, fish and fish eggs (Ebert & Ebert, 2005). Hence, not as comparable to the bronze whaler sharks of this study compared to the larger sand tiger sharks studied by Hussey et al. (2010a). Furthermore, Kim et al. (2012b) fed sharks a diet incorporating

tilapia (*Oreochromis* sp.) which is a freshwater teleost and not accurately representative of a marine food web dynamic. Due to these factors, the values presented by Kim et al. (2012a) and Kim et al. (2012b) were not considered in our analysis.

Bayesian mixing models have been shown to be highly sensitive to assumptions of trophic shift (Bond & Diamond, 2011). Particularly where differences between end members are small (McCutchan et al., 2003). Therefore, the validity of model output is reliant on the accuracy of the TDF applied. The model output of this study was based on the assumptions that a $\Delta\delta^{13}C$ value of 0.4‰ and a $\Delta\delta^{15}N$ value of 2.3‰ were the most accurate TDF values available from the literature for large carnivorous sharks. To be fully confident in our assumptions, actual TDF values for bronze whaler sharks would need to be determined through long-term controlled feeding experiments. However, such testing was not feasible in this study and a surrogate value applied instead.

3.4.5 Mixing Model

The use of a Bayesian mixing model allowed the conversion of isotopic data of potential prey species into food source contributions to the predator diet (Phillips et al., 2014). According to the mixing model, kingfish and piper contributed the greatest proportion to the diet of bronze whaler sharks (mean = 50.7% and 11.5% respectively). Kingfish are a pelagic feeding species found in coastal bays and harbours, around reefs and in open water, but have strong associations to topographic features (Hobday & Campbell, 2009; Francis, 2012). Piper are also found coastally in harbours and shallow embayments where they feed on seagrasses and planktonic crustaceans (Francis, 2012). The dietary contributions of kingfish and piper suggest that bronze whaler sharks derive the majority of their energy from pelagic food webs, rather than from reef and benthos based systems. However, snapper had a similar contribution to piper (mean = 13.8%). Although the mean contribution was greater than that of piper, piper had a greater contribution when looking at the 50 percentile (11.1% compared to 10.8% of snapper) as seen in Figure 3.9 (scaled posterior probabilities) and Table 3.2 (summary statistics table). Like kingfish and piper, snapper are found in inshore shelf habitats, but associate with epibenthic habitats within estuaries, harbours, reefs, and will also feed in the water column although usually not far off the seabed. They are generalist feeders on a wide range of invertebrates such as crabs, worms and shellfish, and small fishes

(Francis, 2012; Compton et al., 2012). The incorporation of snapper into the diet of the bronze whaler sharks also suggests this species has trophic connections to reef and benthic habitats. Because $\delta^{13}C$ values of consumers closely resemble those of the basal carbon source, our data suggests bronze whaler sharks obtain their energy primarily from a coastally-derived pelagic food web.

Jack mackerel and blue mackerel contributed means of only 4.7% and 4.0% respectively to the diet of bronze whaler sharks (Table 3.2). Although blue mackerel occur in coastal pelagic waters, they also inhabit oceanic waters (May & Maxwell, 1986), feeding on planktonic copepods and crustaceans (Francis, 2012). Jack mackerel have a similar diet and distribution to blue mackerel, but adults typically associate to shelf-edge waters (Maxwell, 1979). Coastal waters are typically more enriched in carbon due to the higher productivity found nearshore compared to offshore environments, thus, producing higher $\delta^{13}C$ signatures in consumers utilising coastal food webs (Hill et al., 2006; Graham et al., 2010). This was evident in our data, with blue mackerel and jack mackerel having lower $\delta^{13}C$ values than those found in the other potential prey species. Oceanic phytoplankton (50 km from shore) has previously been reported to have a $\delta^{13}C$ value in the range of -20.0‰ to -21.5‰, while nearshore $\delta^{13}C$ values of 15.4‰ have been documented (Hill et al., 2006). Therefore, it is possible that jack mackerel and blue mackerel utilise resources stemming from a different basal carbon source. The minimal contribution of these species to the predator diet further supports the coastal orientation of bronze whaler sharks when feeding. However, the $\delta^{13}C$ and $\delta^{15}N$ signatures at the base of food webs can vary between biogeographical regions due to geographical differences in nutrient cycling in the lower trophic levels (Graham et al., 2010). Therefore, regionally acquired baselines for each of these environments is required to confirm with confidence the exclusive use of coastal food webs by bronze whaler sharks over offshore communities.

The large dietary contribution of kingfish was an unpredicted outcome, as this species has been found swimming with, and feeding on similar prey species as bronze whaler sharks such as schooling fish (pers. obs.). Animals must consume enough food to meet the energetic demands required for growth and reproduction (Manning et al., 2019). Therefore, predators benefit from selecting prey items that provide the greatest net energy return (Manning et al., 2019). It is known that fish feeding on large prey items dedicate less time on capture, and more time into digesting compared to targeting

smaller prey items (Fall & Fiksen, 2020). Therefore, this close association between the two species may indicate kingfish to be an energetically viable prey option for the sharks, with opportunistic hunting when feeding on similar prey sources allowing maximum energy gain, with minimal energetic cost. Bronze whaler sharks also frequently take kingfish from the lines of boat and spearfishermen (pers. obs.), indicating their interest in this species as a valuable energy source. The low dietary contribution of kahawai (mean = 8.8%; Table 3.2) was also unexpected, as they have previously been found in the stomach contents of bronze whaler sharks along with snapper (pers. obs.). However, stomach contents only provide a snapshot at one point in time of what the organism has recently eaten, and does not provide information on feeding ecology across geographical and temporal scales (Chang et al., 2019). Therefore, stomach contents might miss important prey associations incorporated into the wider diet, and do not reflect the proportional carbon and nitrogen assimilated into the consumer's tissue.

Similar to the results of the mixing model in this study, stomach contents studies have indicated that pelagic teleosts are the most dominant prey group of bronze whaler sharks (Cliff & Dudley, 1992; Lucifora et al., 2009; Rogers et al., 2012). However, these species are typically <35 cm in length (Smale, 1991; Cliff & Dudley, 1992), which differs to that of kingfish found in this study which can grow >100 cm in length (Gillanders et al., 1999). Large-scale stomach contents analysis of bronze whaler sharks has not yet been performed in New Zealand as it has in other regions such as Argentina, South Africa and Australia where there are commercial fisheries for this species. However, it could be beneficial to support the findings of stable isotope analyses and understand potential geographical differences in diet compositions. Previous stomach contents analyses have reported demersal teleosts and cephalopods as other prey items, although a less important component of the overall diet (Cliff & Dudley, 1992; Lucifora et al., 2009). This is similar to the lower dietary proportion of snapper in this study. However, the previously reported consumption of cephalopods indicates the current study potentially missed this prey species in the mixing model analysis. Small elasmobranchs present another potential prey species missing from analysis. One of the assumptions of mixing models is that all prey sources are included in the model (Phillips et al., 2014). This makes them sensitive to missing dietary sources, as dietary contributions must still sum to 100%, causing bias in the contributions of those species that are included when other prey species have been missed (Phillips et al., 2014).

Therefore, the addition of these species to the model may alter the estimated contributions to what was found in this study. However, having too many sources can reduce the discriminatory power of mixing models, so excluding sources should be based on knowledge that excluded species contribute very little to the overall diet of the consumer, with expected biases stipulated in results (Phillips et al., 2014).

It must be noted, that although kingfish and piper were shown to contribute the greatest proportion to the diet of bronze whaler sharks, they also presented the greatest variation around the mean values out of the potential prey species. This indicated that there was greater variability in the isotopic signatures among individuals of these species, which may have been a factor of the relatively small sample sizes of the teleost groups. During the mixing model analysis, using different isotope values of species within their error bounds has the potential to produce a different result in dietary estimates (Phillips, 2012), and needs to be considered when interpreting these results. However, the narrow distribution of the posterior probability curve for kingfish in particular provide some confidence in this result. It is evident that while a powerful method for investigating the trophic dynamics of species, stable isotope analysis may not provide a perfect estimation of the true predator diet on its own (Giménez et al., 2017). Therefore, a multifaceted approach using stable isotope analysis alongside methods such as stomach contents analysis would be beneficial to identify trophic dynamics on different assimilation scales, and how consumption of different prey species may vary through both space and time.

3.4.6 Trophic Position

The trophic position (TP) of an animal is a reflection of the number of energy transfers from primary producers (TP = 1), to herbivores (TP = 2) and into primary (TP = 3), secondary (TP = 4) and tertiary (TP = 5) consumers (Frisch et al., 2014). The number of trophic levels within a community is typically constrained by the insufficient transfer of energy between levels (10% converted into predator production) and population dynamics of a community (Pimm & Lawton, 1977; Heupel et al., 2014).

The trophic position of bronze whaler sharks in this study could not be accurately calculated. This was due to the supporting species' collection not being a perfect representation of community structure, with prey species of teleost, and copepod and

phytoplankton groups unable to be attained during the collection process. Based on the proportion pelagic kingfish and piper contributed to the diet of the bronze whaler shark, plankton present the most likely linkage for bronze whaler sharks to the basal carbon source of the food web, and therefore leave an important gap in the data set.

However, it can be estimated from the difference between the mean $\delta^{15}N$ of bronze whaler sharks (16.6‰) and the microphytobenthos value (5.4‰), i.e., 11.2‰, divided by the presumed TDF per trophic level (2.3‰) that the sharks were at TP of ~4.9. This calculation assumes that phytoplankton have a similar $\delta^{15}N$ to the microphytobenthos as the basal food source. This could be achieved by a food web with 5 trophic levels, comprising phytoplankton (not represented), zooplankton (not represented), planktivorous fish (not represented), first-level piscivores (e.g., mackerel and piper), second-level piscivores (e.g., snapper and tarakihi), culminating in bronze whaler sharks as the top predator (third-level piscivores). Realistically, it can be concluded that bronze whaler sharks in the Bay of Plenty have a trophic position between 4 and 5 (depicted in Appendix 19).

The idea that bronze whaler sharks occupy a trophic position between 4 and 5 aligns with previous estimates of trophic position calculated for this species. Hussey et al. (2015) reported a trophic position of 4.4 for bronze whaler sharks, derived from stable isotope analysis. Similar trophic positions have also been reported for sharks of comparable size. Analysis of stomach contents determined a trophic position of 4.5 ± 0.02SE for dusky sharks (*Carcharhinus obscurus*), and 4.3 ± 0.01SE for scalloped hammerhead (*Sphyrna lewini*) (Hussey et al., 2011). Such estimates place these species as secondary piscivores, indicating they consume smaller piscivorous fish, which in turn consume planktonic species (Hussey et al., 2015). The greater trophic position of sharks over large carnivorous teleost species in the current study was to be expected given the relationship between body size and trophic position, with predators typically being larger than their prey (Hussey et al., 2011). White sharks (*Carcharodon carcharias*) are among the largest of marine predators, and have been estimated to occupy a trophic position of 4.2–5 (Hussey et al., 2012b). Hussey et al. (2012b) reported a significant linear relationship between trophic position and an increase in size. This suggests that juvenile white sharks may share a similar trophic position to bronze whaler sharks, but as they increase in size and incorporate larger prey items into their diet, they may pose a predatory threat to smaller shark species. Considering the

life stage of the bronze whaler sharks in this study, this generalised assessment of trophic position supports the common view that this species, like many other shark species, is an apex predator within the coastal marine community given its trophic positon >4 (Essington et al., 2006). White sharks are also known to utilise similar habitats to bronze whaler sharks within the Bay of Plenty. However, this species is capable of much wider movement patterns, with its predatory role of mature individuals within the region potentially being more transient in nature, and indicates there could be multiple levels within this apex predatory guild. The trophic interactions between bronze whaler sharks and other top predatory shark species in the Bay of Plenty are yet to be identified.

3.4.7 Conclusion

The results of this chapter provide first insight into the population dynamics and trophic ecology of bronze whaler sharks in New Zealand waters. Out of the 40 sharks captured, there was a strong bias towards mature female sharks being caught within coastal environments over summer. This indicated sex segregation, with males potentially utilising different habitats, and potential philopatry of females to coastal sites for reproductive behaviour. Sized based $\delta^{13}C$ and $\delta^{15}N$ profiles did not identify the presence of an ontogenetic shift in $\delta^{13}C$ and $\delta^{15}N$ once sharks had reached maturity. However, differences in trophic position and habitat use may differ in juvenile and sub-adult cohorts which were not represented by the data. The collection of potential prey items, primarily from the coastal region, allowed a Bayesian mixing model to be successfully run to estimate the contributions of teleost species to the diet of bronze whaler sharks in the Bay of Plenty region. Kingfish contributed the greatest proportion to the overall diet of sharks, and alongside the contribution of piper, suggested bronze whaler sharks obtained their energy primarily from a coastally-derived pelagic food web. The incorporation of snapper further supported a coastal orientation as well as trophic links extending to reef and benthic habitats. However, important baseline signatures of plankton were missing, leaving a crucial gap in the data set that was necessary to define basal signatures for inshore and offshore environments. Although data suggests a primary utilisation of coastal sources, these baselines were required to confidently define the exclusive use of coastal food webs over offshore systems by the bronze whaler sharks. Therefore, some uncertainty still remains around these assumptions. The trophic position of sharks also could not be accurately calculated due to the lack of

these plankton-derived baselines. However, an assessment of bivariate $\delta^{13}C$ and $\delta^{15}N$ data indicated bronze whaler sharks have a trophic position between 4 and 5. This aligned with previous trophic position estimates for other similar sized shark species. Trophic analyses are essential if we are to fully understand the role top-level predators play in influencing the structure and function of communities through food web linkages. Although the use of mixing models are not always perfect on their own, they provide a powerful tool when used in conjunction with other methods such as stomach contents analysis to provide information of food web linkages through both short-term and long-term interactions. As a result, stable isotopes provide a valuable tool to enhance our understanding of the feeding ecology and trophic dynamics of species to ensure effective ecosystem-based management of marine communities and fisheries stocks alike.

Chapter 4
Final Discussion

4.1 Overview

The research reported in this thesis adopted a multifaceted approach to investigating the movement behaviour and trophic ecology of bronze whaler sharks (*Carcharhinus brachyurus*) in the Bay of Plenty, New Zealand. Satellite-linked tracking typically provides high-resolution information into the movement patterns of wide-ranging marine predators, with concurrent recordings of environmental conditions such as ambient water temperature and depth beginning to elucidate factors influencing species movements. However, insight into foraging behaviour is difficult to ascertain from satellite tracking alone and this discrepancy is crucial to remedy, if we are to advance our understanding of the ecology of this species. Stable isotope analysis provides an additional method to investigate the habitat use of species', with data generated often complementing findings from tracking studies. In addition, stable isotopes provide insight into the trophic ecology of species, providing important information on energy flow and trophic dynamics within marine communities. Hence, both techniques were employed to provide the first ever examination of the trophic ecology and movement behaviour of bronze whaler sharks. The discussion below examines results from stable isotope analysis that provided contradictory results to the feeding implications of movement data received from satellite-linked tracking.

Despite the transmission rates of satellite-linked tags being low, relatively high transmission accuracies of geolocation estimates allowed the evaluation of movement tracks for each shark, and proved satellite-linked smart positon or temperature transmitting (SPOT5) tags as an efficacious tool when investigating the movement patterns of bronze whaler sharks. Although there were differences in the individual movement tracks of tagged sharks, overall there were similarities in the long-term trends of habitats used. Both shark 55617 and 55620 remained within 2.245 degrees of latitude in waters along the north-eastern region of the North Island, New Zealand, with transmissions being detected no further than the Poor Knights Islands to the north, and Motiti Island to the south. Bronze whaler sharks are known to inhabit coastal

environments around the entirety of the North Island and upper South Island during the summer period. This restriction in movements to a limited stretch of waters along the north-eastern region of the North Island, indicated multiple distinct populations may exist within New Zealand waters. In addition to their restricted range, the recapture of shark 55617 at its original tagging location at Panepane Point, along with the recaptures of three other sharks from the wider study in coastal habitats suggests a level of fidelity to the region. However, due to the small sample size and no male sharks being represented, it could not be determined from the movement data if the New Zealand population is also genetically segregated between regions, or if panmixia occurs. With the sharks using a restricted area of coastal waters, the high number of females compared to males (19:1) caught in coastal habitats throughout the wider study suggest this species may also display a level of natal philopatry. Sex-based differences in habitat use, along with the preference of inshore areas for parturition would have important management implications in protecting bronze whaler shark populations across ontogeny, with vulnerability to anthropogenic activities potentially varying depending on associations to inshore areas based on the age, sex, and reproductive stage of sharks, along with the time of year.

Despite being widely accepted that bronze whaler sharks move away from coastal habitats across their range during winter months, little evidence exists regarding their habitat use and movement patterns during this period when coastal water temperatures cool. Bronze whaler sharks are considered to remain within habitats on the continental shelf in waters no deeper than 200–250 m (Garrick, 1982; Smale, 1991; Cliff & Dudley, 1992; Da Silva & Bürgener, 2007; Benavides et al., 2011; Drew et al., 2016; Bradshaw et al., 2018). However, the data from this study provides first evidence of the importance of shelf-edge and off-shelf habitats to this species during the winter period. For both sharks, autumn (April–June) movements were dominated by location estimates in shelf waters <100 m for shark 55617, and <50 m for shark 55620. However, a change of behaviour was evident from late autumn/winter (July–September), with location estimates during this period then becoming dominated by positions along shelf-edge habitats ~200–500 m depth for shark 55617, and in oceanic waters between 500–1000 m depth for shark 55620 until transmissions for both sharks were lost by early September, 2017. Shark 55620 did return to shelf waters east of Great Barrier Island (~50–100 m depth). However, time spent back in this location was brief, with the shark transmitting back in oceanic waters only six days later, where it remained until

transmissions ceased. Shark 55620 also displayed a distinct shift northward in movements during this winter period.

Despite shifts into shelf-edge and off-shelf habitats, the longitudinal range of both sharks was only 0.975° for shark 55617, and 0.958° for shark 55620. This could have been a factor of the continental shelf extending from the Bay of Plenty region being relatively narrow. Therefore, longitudinal distance travelled necessary to reach oceanic waters was minimal. Further tagging in other regions where distance from mainland New Zealand to the shelf-edge varied, would need to be undertaken to determine if the distance travelled offshore was a factor of shelf size, or distance from mainland coastal regions. The narrow latitudinal and longitudinal ranges reported in this study also suggest that bronze whaler sharks do not undertake transoceanic migrations to nearby land masses such as Australia, as species such as white sharks (*Carcharodon carcharias*) have been shown to perform (Francis et al., 2015a). Genomic investigations into the phylogeography of bronze whaler sharks have shown major discontinuity in gene flow across deep oceanic expanses, lending more weight to the conjecture that this species does not partake in transoceanic migrations (Benavides et al., 2011). However, genetic structure between New Zealand and Australian populations have not been detected indicating that movement across the Tasman Sea (a distance ~2250 km) may occur (Benavides et al., 2011; Junge et al., 2019). Although the tagging data did not indicate the occurrence of transoceanic movements, bronze whaler sharks are capable of travelling distances to at least 2315 km (Rogers et al., 2013), and hence, with the lack of genetic diversity and the presence of multiple stepping-stone habitats between New Zealand and Australia, we cannot eliminate the possibility of such movements. However, the weakness in the genomic analysis by Benavides et al. (2011) was that analysis of the mitochondrial control region haplotypes did not include bi-parentally inherited genetic markers (lacking male-mediated genetic flow), which would be required for identifying weak population sub-divisions, and if genetic patterns reflect the movements of both males and females, or just females. Alternatively, the lack of divergence between these two clades possibly indicates a genetic legacy dating back to the founding of the Australasian population ~160 000 years ago (Benavides et al., 2011). Bi-parent genetic markers would also need to be analysed to detect if genetic sub-structure within the New Zealand population also exists. The restricted range in movements and apparent fidelity to coastal regions over summer in tagged females suggests genetically distinct sub-populations could be the case. However, males are not

necessarily restricted by the same reproductive needs, such as suitable pupping habitat for females. Therefore, male mediated gene flow could occur over greater geographical ranges rather than being restricted to a particular region or landmass. If genetic connectivity exists between New Zealand and Australia as suggested by Benavides et al. (2011), the Australasian population is subject to varying management regimes, which if not recognised by fisheries models could ultimately result in population declines across the entire south-west Pacific group, and not just in Australia where it is subject to a commercial fishery.

A number of factors can be responsible for the large-scale and seasonal movement patterns observed in some shark species. Temperature in particular can be a major driver influencing species distributions (Kohler & Turner, 2001). Overall, shark 55617 and 55620 both experienced a wide range of ambient water temperatures between 12–22°C. However, a narrower temperature preference between 16– 20°C for shark 55617, and 16–22°C for shark 55620 was evident. At the time of tagging, the beginning of April, coastal water temperatures were around 20–21°C and dropped to as low as 13.8°C during winter. However, during winter, shark 55617 primarily remained in waters between 14–18°C and shark 55620 between 16–18°C. It was suspected that the movement of bronze whaler sharks to shelf and oceanic waters was in response to a thermal cue as coastal temperatures declined with the onset of winter. By the time both sharks were transmitting from offshore locations, coastal water temperatures had decreased to around 15°C, suggesting a thermal threshold driving the seasonal movements in this species. Inshore water temperatures below 15°C have also been shown to coincide with low detections of bronze whaler sharks tracked with acoustic tags in the Gulf of St. Vincent, Australia (Drew et al., 2019). Furthermore, temperatures above 16°C have been shown to be important for the presence of bronze whaler sharks in Anegada Bay, Argentina (Lucifora et al., 2005), indicating a similar response to temperature of this species across its range. However, both sharks spent a relatively small amount of time in waters between 12–14°C (Shark 55617, 0.06%; Shark 55620, 0.01%). The recording of cooler ambient water temperatures was thought to be due to either a return to inshore waters, or travelling at depth between locations. However, the low number of transmissions and discontinuous retrieval of temperature data made it difficult to determine such movements.

The findings from the stable isotope analysis somewhat contradicted movement and feeding location implications attained from satellite-linked tracking. Because the isotopic ratio of carbon (C^{13}:C^{12}) varies little with successive trophic transfers, $\delta^{13}C$ values can provide a valuable indicator of foraging habitat used (Layman et al., 2007a; Li et al., 2016). A qualitative assessment of bivariate $\delta^{13}C$ and $\delta^{15}N$ values for each species provided first indication that bronze whaler sharks assimilate the majority of their energy through the utilisation of a coastally-derived food web. This was evident from the mean $\delta^{13}C$ values of the bronze whaler sharks falling within the range of those of coastal microphytobenthos, and teleost, invertebrate, and macro algae species. The utilisation of coastal food webs by bronze whaler sharks was further supported by the quantitative assessment of the relative contributions of potential prey species to the diet of the sharks using a Bayesian mixing model. Potential prey species used in the model included kahawai (*Arripis trutta*), kingfish (*Seriola lalandi*), piper (*Hyporhamphus ihi*), snapper (*Pagrus auratus*), tarakihi (*Nemadactylus macropterus*), blue mackerel (*Scomber australasicus*), and jack mackerel (*Trachurus declivis*). Potential prey species selection was based on knowledge from previous studies of stomach contents analysis in populations from Australia (Rogers et al., 2012), South Africa (Smale, 1991; Cliff & Dudley, 1992) and Argentina (Lucifora et al., 2009), sample availability, and local knowledge gained through a small number of necropsies performed on beach-cast specimens in New Zealand. When a trophic discrimination factor of +0.4‰ for $\delta^{13}C$ and +2.3‰ for $\delta^{15}N$ (McCutchan et al., 2003) was applied to the model, bronze whaler shark values fell within the end members of adjusted prey species providing confidence in the selection of potential prey species, and that the model was likely to converge.

Kingfish and piper contributed the greatest proportion, accounting for a mean of 50.7% and 11.5% of the bronze whaler shark diet respectively. The greater dietary contributions of pelagic teleosts aligns with findings from stomach contents analysis studies on populations from Argentina (Lucifora et al., 2009), South Africa (Cliff & Dudley, 1992), and Australia (Rogers et al., 2012). However, these studies identified that pelagic teleosts were typically <35 cm in length compared to kingfish which can exceed 100 cm (Smale, 1991; Cliff & Dudley, 1992; Gillanders et al., 1999). The incorporation of kingfish into the diets of sharks in this study suggests geographical differences in prey selection may exist in this species. The large dietary contribution of kingfish may also be a factor of scavenging from boat and spearfishermen in the region. Snapper were also an important component of the bronze whaler shark diet (mean =

13.8%), indicating trophic links also extend into epibenthic habitats. Interestingly, jack mackerel and blue mackerel, which inhabit shelf and oceanic waters, contributed proportions of only 4.7% and 4.0% respectively to the diet of bronze whaler sharks. The dietary contributions of teleost species further suggest that bronze whaler sharks obtain their energy primarily from a coastally-derived food web rather than offshore food sources. However, it must be noted that small elasmobranchs and cephalopod species were not represented in the mixing model analysis, which may have created bias in estimated contributions of species that were included due to the sensitivity of the model to missing dietary sources. A different result may have also eventuated if informative priors from regionally derived stomach contents analysis were incorporated into the model. Furthermore, the lack of appropriate regionally acquired food web baseline signatures for $\delta^{13}C$ prevented the ability to confirm with confidence that bronze whaler sharks were exclusively utilising a coastally-derived food web over offshore communities. Although some uncertainties remain around the data presented here, the suggestion of trophic links to inshore food webs raises the question of whether or not the sharks feed when in shelf-edge and offshore habitats. The long period of time the two tagged sharks spent in this offshore environment indicate they are likely to consume a prey source at some point in these locations to meet energy requirements. However, it is possible that any consumption of offshore prey species is only a minor amount relative to coastally-derived sources, and thus, is not reflected in the isotopic signatures of their tissues. Time spent in offshore habitats suggest bronze whaler sharks also induce an indirect behavioural predatory influence in oceanic prey communities.

A number of biotic and abiotic factors can influence animal movements, with home range size and residency reflecting habitat quality and food availability, intra- and inter-specific competition, protection from predators and accessibility to mates and nursery habitats (Papastamatiou et al., 2010). Satellite-linked tagging data indicated that temperature was potentially a driving force behind movements away from the coastline during the winter period. This could be in response to maintaining optimal thermoregulatory requirements. However, as bronze whaler sharks are top-level predators, their change in distribution over this period could also be in response to seasonal changes in distributions of prey species, with inshore waters typically more productive during the summer period compared to the winter months. However, further understanding of predator-prey associations and seasonal movements of prey species would be required to test this relationship. The indication of sex segregation with males

primarily utilising habitats away from inshore environments also raises the consideration that offshore movements by females could be related to mating behaviour. However, understanding of male movements also would be required to establish the spatial and temporal co-ordination of such events, and whether it occurs in offshore waters.

The notably larger enrichment in $\delta^{15}N$ of a predator relative to its diet provides a continuous measure of assimilated energy throughout a food web, allowing the trophic position of an animal to be calculated and food chain length to be estimated (Post, 2002; Li et al., 2016). The lack of appropriate planktonic baseline signatures for $\delta^{15}N$ also restricted the ability to accurately calculate the trophic position of bronze whaler sharks sampled in this study. However, assessment of bivariate $\delta^{13}C$ and $\delta^{15}N$ data under the assumption that phytoplankton had a similar $\delta^{15}N$ value to microphytobenthos (5.4‰) as the basal food source, indicated bronze whaler sharks occupy a trophic position between 4 and 5. The tropic level estimation and the position of bronze whaler sharks relative to other species within the isospace matrix support its apex level status within associated marine communities. This was further supported through similarities in this study's trophic level estimation with a previous trophic level of 4.4 calculated for bronze whaler sharks (Hussey et al., 2015), along with similarities with other shark species of a similar size – also considered apex predators within the marine space (Hussey et al., 2011). The morphological and ecological characteristics of bronze whaler sharks additionally match definitions described within the literature, such as large-bodied, encompassing a large home range, and occupying the highest trophic tier within their community (Heupel et al., 2014). Although tagged sharks in this study revealed a level of restriction in their movements, they demonstrated movement patterns across multiple environments and their potential in connecting energy flow across multiple habitats over broad spatial scales, compared to smaller mesopredator species that may show fidelity to a particular reef system for example.

The connection of bronze whaler sharks to multiple trophic links within the food web also suggested a high level of influence over community function. Therefore, if removed, the loss of bronze whaler sharks from the coastal marine system could trigger cascading effects through lower levels of the food web and across multiple trophic links. However, if large mature females are shifting away from coastal systems during the winter period, the top-down predatory effects of this species on the wider coastal system

would also be lost. The persistence of coastal systems year round could indicate a high level of complexity within coastal food webs, with the more weakly interacting trophic links playing an important role in buffering the loss of the stronger trophic link from the bronze whaler sharks. Alternatively, when the bronze whaler sharks leave the coastal environment, another functionally equivalent species from the predator guild may replace the temporally absent species, indicating a level of intra-guild functional diversity of shark assemblages and temporal redundancy in bronze whaler sharks within coastal systems. However, research suggests this is not the case, with identification of a high level of trophic structure and limited functional equivalence previously identified within top predatory shark assemblages (Hussey et al., 2015). A number of large predatory shark species can be found in New Zealand waters. However, the inter-species variability and potential trophic overlap between these species remain unknown. Understanding the dynamics of this top predatory guild is important if we are to understand the trophic linkages throughout food webs, and the potential cascading effects on the wider system when apex predator populations decline below a threshold past which, their functional influence on food web structure and function are lost.

4.2 Future Recommendations

Because this thesis presented the first use of satellite tracking combined with use of stable isotope analysis to investigate the movement behaviour and wider trophic dynamic of bronze whaler sharks, it provides an important stepping-stone and future direction to further our understanding of the movement and trophic ecology of this species.

The greatest limitation of satellite tracking was the small sample size, with only two mature female bronze whaler sharks represented. Research presented here confirms that SPOT5 tags are effective in informing the spatial and temporal movement patterns of this species, hence it would be beneficial now to tag a larger number of sharks to elucidate if the movement patterns observed in this study are representative of the wider population. Only mature females were the subjects of this research, with the absence of males, possibly a function of segregation of the sexes as adults, and juveniles as they transition from nursery habitats into the adult population, resulting in data gaps in our understanding of differences in habitat use between sexes and across ontogeny. Representation of male and juvenile cohorts is important if we are to understand

ecological differences within population groups, and is argued to be of high importance for informing conservation management. A greater, more representative sample size would also provide more confidence in assumptions of home range size and population connectivity throughout New Zealand waters, and may identify particular regions as ecological hotspots and where particular predatory influence over habitats is exerted. The tagging of individuals from different geographical regions within New Zealand waters would also be beneficial to investigate if the winter movements offshore are consistent throughout the New Zealand population, and if the lateral extent of the continental shelf from the coast is a factor determining distance travelled from mainland coastal habitats. Further investigation into home range size and population connectivity would also be supported through analysis of extensive tag and release data collected by the Ministry for Primary Industries dart tagging program. In addition, analysis of bi-parent genetic markers of a large number of individuals from broad geographical areas would identify the level of reproductive mixing between what is currently expected to be multiple segregated populations around New Zealand. This could also be applied to populations in Australia to further understand genetic structure within the Australasian region.

The understanding of the seasonal use of inshore waters could also be supported through the use of Baited Remote Underwater Video Systems (BRUVS), which if deployed throughout all seasons, could help identify if differences in species abundances between summer and winter in inshore habitats truly does exist. Furthermore, the use of BRUVS would support the establishment of important baselines on population abundance for this species. Because BRUVS sample all species that come into view of the camera unit, this technique would also provide valuable information on the diversity and abundance of other shark species and prey assemblages of the different habitats surveyed, which is lacking in the Bay of Plenty region.

While it was assumed bronze whaler sharks did not perform diving behaviour, the addition of depth sensors to the tag unit would further our understanding of not only the horizontal movements of this species, but also its vertical movements within the water column and how that may relate to prey assemblages, bathymetry and behaviour. To avoid permanent structural fin damage, it is recommended that pop-up satellite archival tags (PSAT's) be tested, as they can be anchored into the dorsal musculature rather than

attachment to the first dorsal fin, and would be more suitable for use on younger, smaller individuals of the population.

While stable isotope analysis presented a greater sample size, this technique was still met with biases with data representing 38 mature females and only two mature males. As with the satellite tagging, no juveniles or sub-adults from either sex were represented by this data. Future stable isotope analyses would also benefit from better representation of these population groups so changes in trophic dynamics and influences on food webs with sex and across ontogeny could be better understood. Although the findings from stable isotope analysis suggested the primary use of a coastally-derived food web by bronze whaler sharks, the lack of regionally acquired planktonic baselines for both inshore and offshore environments prevented the ability to properly confirm this hypothesis and elucidate some uncertainty around the contradictory results reported by the two methods adopted by this research. The inclusion of phytoplankton and zooplankton collected from both inshore and offshore habitats into analysis would provide distinct baseline signatures required to determine the exclusive or shared utilisation of these habitats by the sharks.

Whilst the collection of potential prey species was adequate in providing suitable end members in relation to the $\delta^{13}C$ and $\delta^{15}N$ values of the bronze whaler sharks, stomach contents analyses from other geographical regions suggests that small elasmobranchs and cephalopods were missed as potential prey species in this study's mixing model analysis. The addition of these species might influence the interpretation of results found by the present analysis, and remove any potential biases toward the proportional contributions of species that were included. Furthermore, the collection of larger sample sizes of potential preys species may reduce concerns around potential error in the mixing model stemming from the greater variance of $\delta^{13}C$ and $\delta^{15}N$ values of potential prey species. Large-scale stomach contents analysis in New Zealand populations would help us to better understand potential geographical differences in prey species consumed, and provide a more relevant informative prior to be incorporated into the model.

Where species have similar roles in maintaining the structure and function of associated systems, a level of ecosystem resilience exists where other species can fill the predatory roles of species which are removed. A number of shark species utilise shelf habitats

within New Zealand, such as (but not exclusive to) mako (*Isurus oxyrinchus*), blue (*Prionace glauca*), white, thresher (*Alopias vulpinus*), smooth hammerhead (*Sphyrna zygaena*), seven gill (*Notorynchus cepedianus*), school (*Galeorhinus galeus*) and rig (*Mustelus lenticulatus*) sharks. Expanding stable isotope analyses into the wider predator guild would help to understand if inter-species structure and niche partitioning between shark species exists, and what that may mean for the wider food web when seasonal shifts in shark movements occur. A larger, more diverse species collection from offshore food web systems would also help to elucidate trophic relationships between species, and allow mixing model analyses for multiple shark species to identify where niche overlaps may occur. Furthermore, the appropriate collection of $\delta^{15}N$ baseline signatures would allow more accurate calculation of the trophic position of bronze whaler sharks against other shark species and potential prey species from the region.

4.3 Concluding Statement

Understanding the food web dynamics of marine communities is a complex issue. In order to effectively inform management, identification of the spatial and temporal distributions of species, along with species associations within and between trophic tiers is required. This is particularly true for top-level predators such as sharks, given their importance in sustaining marine ecosystems and their vulnerability to multiple anthropogenic threats. This thesis adopted a multidisciplinary approach to investigate the habitat use and trophic ecology of the relatively understudied bronze whaler shark. Novel information on seasonal movement behaviour was provided through the use of satellite-linked smart position or temperature transmitting (SPOT5) tags, revealing previously unknown movements from shelf waters into shelf-edge and oceanic environments. Temperature preferences were also identified, with a shift from coastal habitats with the onset of the winter period associated with a decline of inshore water temperature below 15°C. However, stable isotope analysis revealed contradictory results with a reliance on coastally-derived carbon sources evident through evaluation of bivariate $\delta^{13}C$ and $\delta^{15}N$ stable isotope signatures, and proportional estimations of prey sources to the diet of bronze whaler sharks through the use of a Bayesian mixing model. However, uncertainties remain in the analyses presented here due to the lack of regionally acquired planktonic baselines for both inshore and offshore environments, preventing the ability to fully exclude the use of offshore food webs with certainty. The

lack of appropriate $\delta^{15}N$ baselines also prevented accurate assessment of trophic position. However, estimations from available data indicated bronze whaler sharks occupied a trophic position between 4 and 5, which aligned with previous estimates calculated for this species, and other shark species of a similar size. This research provides an important stepping-stone in increasing our knowledge on this important apex predator within both New Zealand, and marine environments across its range. It is evident that the ecology of bronze whaler sharks is complex, with a wide scope for future research across multiple disciplines. An understanding of population baselines, species movement patterns, and trophic roles within marine communities is crucial if scientists are to determine the importance of sharks within marine environments, their wider ecosystem dynamics, and potential trophic cascades which may result from the large-scale removal of these top predatory species from marine ecosystems. Such information can consequently inform effective species and ecosystem-based management plans within and across different jurisdictional boundaries, factoring in concerns and calls for enhanced resilience in marine dynamics expressed by the various commercial, recreational and cultural sectors that rely on the persistence of marine species.

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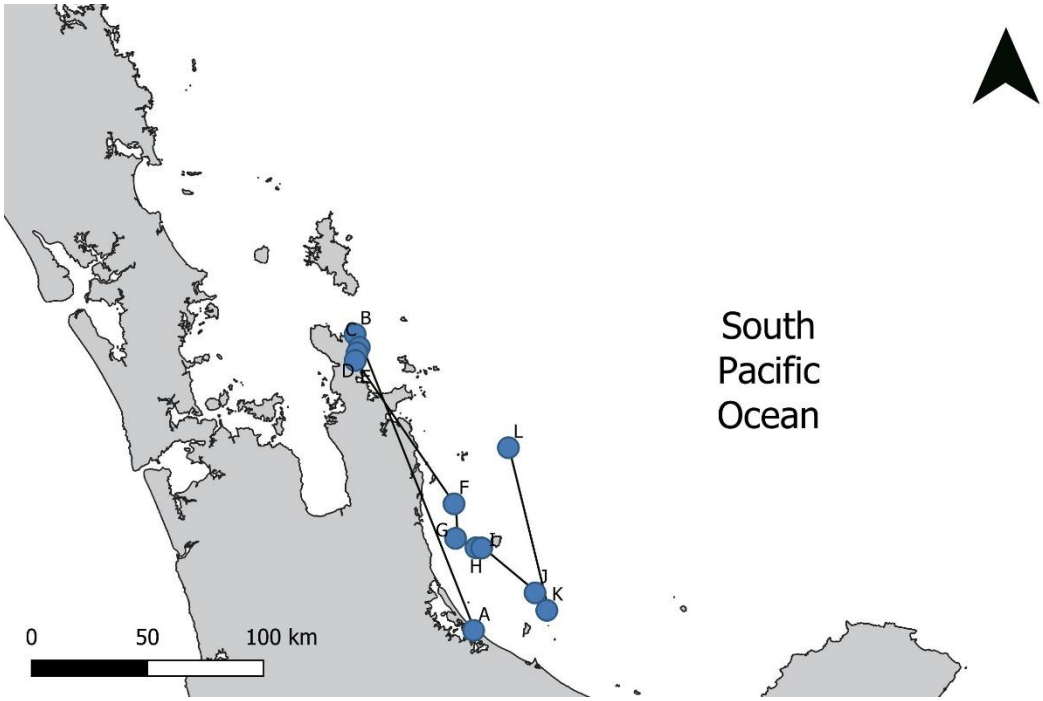
Appendices

Appendix 1: Tracking data for shark 55617, tagged with a satellite-linked smart position or temperature transmitting (SPOT5) tag in north-eastern New Zealand, 2017. Figure shows total track comprised of vectors between transmission locations labelled A – L, with corresponding movement data in table.

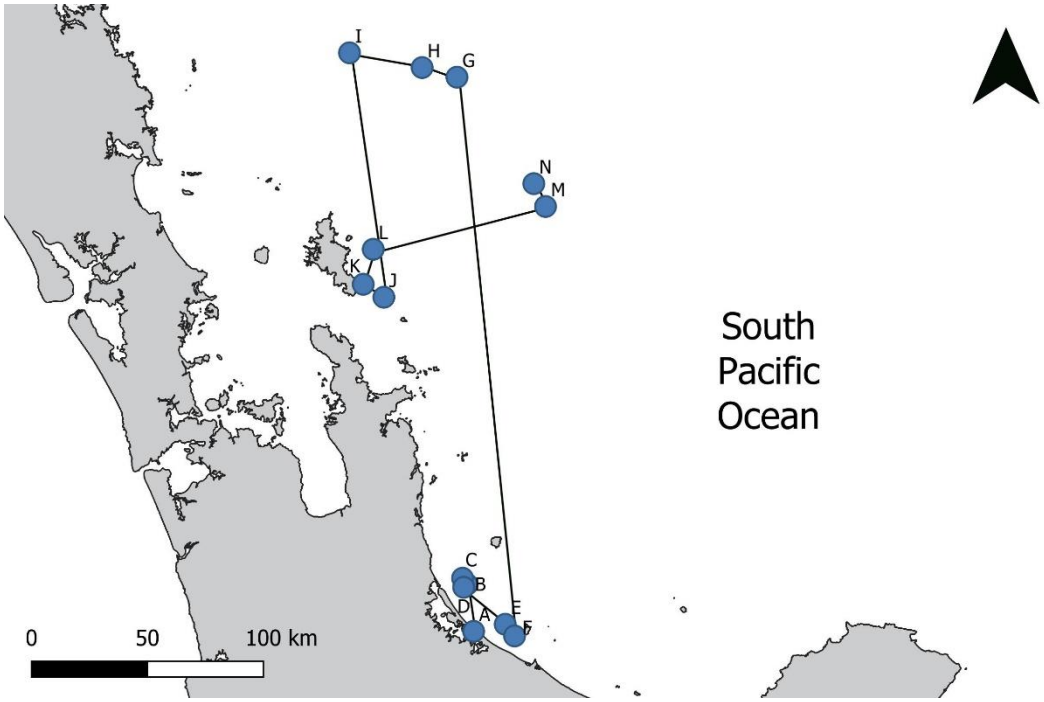


Map produced using Quantum GIS (v3.16, Hannover). Spatial data obtained from DIVA-GIS. CRS: WGS84 (EPSG 4326).

Appendix 1 continued.

Transmission	Latitude	Longitude	Quality	Time	Date	Location	Distance (km)	Distance (m)	Direction	Time (hrs)	Time (sec)	Speed (km/h)	Speed (m/s)	Speed (TL/s)
A	-37.638	176.162		1505	1/04/2017									
B	-36.500	175.541	2	630	10/05/2017	A - B	137.84	137840	NW	927.417	3338700	0.149	0.041	0.014
C	-36.550	175.563	B	100	12/05/2017	B - C	5.89	5890	S	42.5	153000	0.139	0.038	0.013
D	-36.572	175.553	2	243	12/05/2017	C - D	2.60	2600	S	1.717	6180	1.514	0.421	0.142
E	-36.602	175.545	B	942	12/05/2017	D - E	3.41	3410	S	6.983	25140	0.488	0.136	0.046
F	-37.148	176.045	A	835	17/05/2017	E - F	75.22	75220	SE	118.883	427980	0.633	0.176	0.059
G	-37.282	176.058	3	2356	18/05/2017	F - G	14.92	14920	S	39.35	141660	0.379	0.105	0.035
H	-37.316	176.159	2	808	19/05/2017	G - H	9.72	9720	E	8.2	29520	1.185	0.329	0.111
I	-37.316	176.187	1	849	19/05/2017	H - I	2.48	2480	E	0.683	2460	3.631	1.008	0.339
J	-37.483	176.455	A	1537	20/06/2017	I - J	30.11	30110	SE	774.8	2789280	0.039	0.011	0.004
K	-37.549	176.516	B	2227	5/07/2017	J - K	9.10	9100	SE	366.833	1320600	0.025	0.007	0.002
L	-36.922	176.299	1	1440	5/09/2017	K - L	72.20	72200	N	1480.217	5328780	0.049	0.014	0.005

Appendix 2: Tracking data for shark 55620, tagged with a satellite-linked smart position or temperature transmitting (SPOT5) tag in north-eastern New Zealand, 2017. Figure shows total track comprised of vectors between transmission locations labelled A – N, with corresponding movement data in table.



Map produced using Quantum GIS (v3.16, Hannover). Spatial data obtained from DIVA-GIS. CRS: WGS84 (EPSG 4326).

Appendix 2 continued.

Transmission	Latitude	Longitude	Quality	Time	Date	Location	Distance (km)	Distance (m)	Direction	Time (hrs)	Time (sec)	Speed (km/h)	Speed (m/s)	Speed (TL/s)
A	-37.638	176.162		920	8/04/2017									
B	-37.456	176.122	1	1938	19/04/2017	A - B	20.51	20510	N	274.3	987480	0.075	0.021	0.007
C	-37.433	176.099	1	2042	19/04/2017	B - C	3.26	3260	NW	1.067	3840	3.055	0.849	0.297
D	-37.468	176.106	B	1828	21/04/2017	C - D	3.93	3930	S	45.767	164760	0.086	0.024	0.008
E	-37.606	176.315	1	2208	9/05/2017	D - E	24.00	24000	SE	435.667	1568400	0.055	0.015	0.005
F	-37.650	176.363	A	938	12/05/2017	E - F	6.47	6470	SE	59.5	214200	0.109	0.030	0.011
G	-35.487	175.990	2	933	21/07/2017	F - G	242.34	242340	N	1679.917	6047700	0.144	0.040	0.014
H	-35.454	175.823	3	1719	27/07/2017	G - H	15.59	15590	W	151.767	546360	0.103	0.029	0.010
I	-35.405	175.476	B	827	29/07/2017	H - I	31.98	31980	W	39.133	140880	0.817	0.227	0.079
J	-36.351	175.674	A	624	8/08/2017	I - J	106.48	106480	S	237.95	856620	0.447	0.124	0.043
K	-36.303	175.573	B	1813	8/08/2017	J - K	10.52	10520	NW	11.817	42540	0.890	0.247	0.086
L	-36.166	175.616	A	2037	8/08/2017	K - L	15.69	15690	N	2.4	8640	6.538	1.816	0.635
M	-35.977	176.434	3	1712	14/08/2017	L - M	76.61	76610	E	140.583	506100	0.545	0.151	0.053
N	-35.890	176.374	B	1724	31/08/2017	M - N	11.07	11070	NW	408.2	1469520	0.027	0.008	0.003

Appendix 3: Summary of percentage time-at-temperature data received for shark 55617 tagged with a satellite-linked smart position or temperature transmitting (SPOT5) tag in north-eastern New Zealand, 2017.

Date	<8°C	8-10°C	10-12°C	12-14°C	14-16°C	16-18°C	18-20°C	20-22°C	22-24°C	24-26°C	26-28°C	>28°C
7/04/2017 18:00	0	0	0	0	0	0	0	100	0	0	0	0
22/04/2017 6:00	0	0	0	0	0	0	54.2	45.8	0	0	0	0
4/05/2017 6:00	0	0	0	0	0	18.4	81.6	0	0	0	0	0
4/05/2017 18:00	0	0	0	0	0	0	100	0	0	0	0	0
5/05/2017 6:00	0	0	0	0	0	0	100	0	0	0	0	0
6/05/2017 6:00	0	0	0	0	0	3.9	96.1	0	0	0	0	0
6/05/2017 18:00	0	0	0	0	0	0	100	0	0	0	0	0
7/05/2017 18:00	0	0	0	0	0	0	100	0	0	0	0	0
8/05/2017 6:00	0	0	0	0	0	0	100	0	0	0	0	0
9/05/2017 6:00	0	0	0	0	0	0	100	0	0	0	0	0
10/05/2017 6:00	0	0	0	0	0	0	100	0	0	0	0	0
12/05/2017 18:00	0	0	0	0	0	0	100	0	0	0	0	0
13/05/2017 6:00	0	0	0	0	0	0	100	0	0	0	0	0
13/05/2017 18:00	0	0	0	0	0	0	100	0	0	0	0	0
14/05/2017 6:00	0	0	0	0	0	0	100	0	0	0	0	0
14/05/2017 18:00	0	0	0	0	0	0	100	0	0	0	0	0
15/05/2017 18:00	0	0	0	0	0	9.6	90.4	0	0	0	0	0
16/05/2017 6:00	0	0	0	0	0	0	100	0	0	0	0	0
16/05/2017 18:00	0	0	0	0	0	2.8	97.2	0	0	0	0	0
18/05/2017 6:00	0	0	0	0	0	2.4	97.6	0	0	0	0	0
22/05/2017 6:00	0	0	0	0	0	0	100	0	0	0	0	0
29/05/2017 6:00	0	0	0	0	0	8.1	91.9	0	0	0	0	0
7/06/2017 6:00	0	0	0	0	0	84.4	15.6	0	0	0	0	0

Date	<8°C	8-10°C	10-12°C	12-14°C	14-16°C	16-18°C	18-20°C	20-22°C	22-24°C	24-26°C	26-28°C	>28°C
14/06/2017 6:00	0	0	0	0	0	100	0	0	0	0	0	0
14/06/2017 18:00	0	0	0	0	0	100	0	0	0	0	0	0
15/06/2017 6:00	0	0	0	0	0	100	0	0	0	0	0	0
15/06/2017 18:00	0	0	0	0	1.2	98.8	0	0	0	0	0	0
16/06/2017 6:00	0	0	0	1.2	2	96.9	0	0	0	0	0	0
17/06/2017 6:00	0	0	0	0	0	100	0	0	0	0	0	0
17/06/2017 18:00	0	0	0	0	0	100	0	0	0	0	0	0
18/06/2017 6:00	0	0	0	0	0	100	0	0	0	0	0	0
19/06/2017 6:00	0	0	0	0	0	100	0	0	0	0	0	0
29/06/2017 18:00	0	0	0	0	0	100	0	0	0	0	0	0
2/07/2017 6:00	0	0	0	0	0	100	0	0	0	0	0	0
2/07/2017 18:00	0	0	0	0	0	100	0	0	0	0	0	0
8/08/2017 6:00	0	0	0	0	9.2	90.8	0	0	0	0	0	0
14/08/2017 18:00	0	0	0	0	100	0	0	0	0	0	0	0
15/08/2017 18:00	0	0	0	0	0	100	0	0	0	0	0	0
16/08/2017 6:00	0	0	0	0	8.9	91.1	0	0	0	0	0	0
31/08/2017 18:00	0	0	0	0	2.4	97.6	0	0	0	0	0	0
1/09/2017 6:00	0	0	0	0	0	100	0	0	0	0	0	0
1/09/2017 18:00	0	0	0	0	0	100	0	0	0	0	0	0
2/09/2017 18:00	0	0	0	0	80.6	19.4	0	0	0	0	0	0
3/09/2017 6:00	0	0	0	0	100	0	0	0	0	0	0	0
10/09/2017 18:00	0	0	0	0	99.6	0.4	0	0	0	0	0	0
11/09/2017 18:00	0	0	0	0	100	0	0	0	0	0	0	0
12/09/2017 6:00	0	0	0	1.6	98.4	0	0	0	0	0	0	0
8/01/2018 6:00	0	0	0	0	0	0	12.2	87.8	0	0	0	0
% Frequency	**0**	**0**	**0**	**0.06**	**12.55**	**40.10**	**42.43**	**4.87**	**0**	**0**	**0**	**0**

Appendix 4: Summary of percentage time-at-temperature data received for shark 55620 tagged with a satellite-linked smart position or temperature transmitting (SPOT5) tag in north-eastern New Zealand, 2017.

Date	<8°C	8-10°C	10-12°C	12-14°C	14-16°C	16-18°C	18-20°C	20-22°C	22-24°C	24-26°C	26-28°C	>28°C
11/04/2017 6:00	0	0	0	0	0	0	22.7	77.3	0	0	0	0
11/04/2017 18:00	0	0	0	0	0	0	0	100	0	0	0	0
12/04/2017 18:00	0	0	0	0	0	0	0	100	0	0	0	0
13/04/2017 6:00	0	0	0	0	0	0	4.3	95.7	0	0	0	0
13/04/2017 18:00	0	0	0	0	0	0	17.5	82.5	0	0	0	0
14/04/2017 6:00	0	0	0	0	0	0	13.9	86.1	0	0	0	0
14/04/2017 18:00	0	0	0	0	0	0	56	44	0	0	0	0
15/04/2017 6:00	0	0	0	0	0	0	31.7	68.3	0	0	0	0
15/04/2017 18:00	0	0	0	0	0	0	24.7	75.3	0	0	0	0
16/04/2017 6:00	0	0	0	0	0	0	0	100	0	0	0	0
16/04/2017 18:00	0	0	0	0	0	0	5.6	94.4	0	0	0	0
17/04/2017 6:00	0	0	0	0	0	0	29.2	70.8	0	0	0	0
18/04/2017 6:00	0	0	0	0	0	0	77.7	22.3	0	0	0	0
18/04/2017 18:00	0	0	0	0	0	0	28.8	71.2	0	0	0	0
19/04/2017 18:00	0	0	0	0	0	0	70.8	29.2	0	0	0	0
20/04/2017 6:00	0	0	0	0	0	0	23.8	76.2	0	0	0	0
5/05/2017 18:00	0	0	0	0	0	0	100	0	0	0	0	0
6/05/2017 6:00	0	0	0	0	0	0	100	0	0	0	0	0
6/05/2017 18:00	0	0	0	0	0	0	100	0	0	0	0	0
7/05/2017 6:00	0	0	0	0	0	1.6	98.4	0	0	0	0	0
7/05/2017 18:00	0	0	0	0	0	0	100	0	0	0	0	0
8/05/2017 6:00	0	0	0	0	0	0	100	0	0	0	0	0
8/05/2017 18:00	0	0	0	0	0	0	100	0	0	0	0	0
10/05/2017 18:00	0	0	0	0	0	0	100	0	0	0	0	0
14/07/2017 18:00	0	0	0	0	2	98	0	0	0	0	0	0
15/07/2017 18:00	0	0	0	0	0	100	0	0	0	0	0	0

Appendix 4 continued.

Date	<8°C	8-10°C	10-12°C	12-14°C	14-16°C	16-18°C	18-20°C	20-22°C	22-24°C	24-26°C	26-28°C	>28°C
16/07/2017 6:00	0	0	0	0	0	100	0	0	0	0	0	0
16/07/2017 18:00	0	0	0	0	0	100	0	0	0	0	0	0
19/07/2017 6:00	0	0	0	0	0	100	0	0	0	0	0	0
19/07/2017 18:00	0	0	0	0	0	100	0	0	0	0	0	0
20/07/2017 18:00	0	0	0	0	0	100	0	0	0	0	0	0
24/07/2017 18:00	0	0	0	0	0	100	0	0	0	0	0	0
25/07/2017 6:00	0	0	0	0	0	100	0	0	0	0	0	0
25/07/2017 18:00	0	0	0	0	0	100	0	0	0	0	0	0
26/07/2017 6:00	0	0	0	0	0	100	0	0	0	0	0	0
3/08/2017 6:00	0	0	0	0	3.9	96.1	0	0	0	0	0	0
3/08/2017 18:00	0	0	0	0	34.9	65.1	0	0	0	0	0	0
4/08/2017 6:00	0	0	0	0.6	51.7	47.7	0	0	0	0	0	0
4/08/2017 18:00	0	0	0	0	70	30	0	0	0	0	0	0
5/08/2017 18:00	0	0	0	0	100	0	0	0	0	0	0	0
6/08/2017 6:00	0	0	0	0	100	0	0	0	0	0	0	0
6/08/2017 18:00	0	0	0	0	100	0	0	0	0	0	0	0
11/08/2017 6:00	0	0	0	0	0	100	0	0	0	0	0	0
12/08/2017 6:00	0	0	0	0	0	100	0	0	0	0	0	0
13/08/2017 6:00	0	0	0	0	0	100	0	0	0	0	0	0
16/08/2017 6:00	0	0	0	0	18.1	81.9	0	0	0	0	0	0
17/08/2017 18:00	0	0	0	0	5.6	94.4	0	0	0	0	0	0
18/08/2017 18:00	0	0	0	0	13.9	86.1	0	0	0	0	0	0
24/08/2017 6:00	0	0	0	0	13.9	86.1	0	0	0	0	0	0
27/08/2017 18:00	0	0	0	0	0	100	0	0	0	0	0	0
28/08/2017 6:00	0	0	0	0	3.1	96.9	0	0	0	0	0	0
29/08/2017 6:00	0	0	0	0	2.4	97.6	0	0	0	0	0	0
30/08/2017 18:00	0	0	0	0	0	100	0	0	0	0	0	0
% Frequency	**0**	**0**	**0**	**0.01**	**9.80**	**44.93**	**22.74**	**22.52**	**0**	**0**	**0**	**0**

Appendix 5: Summary of recapture data from dart tagging of bronze whaler sharks (*Carcharhinus brachyurus*) in the Bay of Plenty, New Zealand.

Tag Number	Initial tagging date	Initial tagging location	Recapture date	Recapture location	Time at liberty (days)
ST 55617 / DT G156338	1/04/2017	Panepane Point	23/09/2018	Panepane Point	539
DT G156332	17/03/2017	Lower Harbour	6/05/2017	Panepane Point	49
DT G156324	23/01/2017	Papamoa Beach	22/01/2018	Papamoa Beach	365
DT G156343	8/04/2017	Panepane Point	17/02/2018	Panepane Point	315

ST = SPOT5 tag
DT = Conventional dart tag

Appendix 6: Summary of capture and stable isotope data of bronze whaler sharks (*Carcharhinus brachyurus*) in the Bay of Plenty, New Zealand.

Shark	Date	Location	TL_{flex} (cm)	Sex	% C	$\delta^{13}C$	$\delta^{13}C$*	%N	$\delta^{15}N$	C:N
1	18/11/2016	Upper Harbour	236	F	49.65	-16.47	-16.48	14.84	17.05	3.35
2	18/11/2016	Upper Harbour	251	F	50.27	-15.68	-15.60	14.67	16.27	3.43
3	1/12/2016	Upper Harbour	275	F	50	-16.00	-15.99	14.85	16.80	3.37
4	1/12/2016	Upper Harbour	295	F	49.68	-15.88	-15.84	14.64	16.38	3.39
5	13/12/2016	Upper Harbour	260	F	50.9	-15.88	-15.80	14.79	16.95	3.44
6	18/12/2016	Panepane	251	F	44.67	-16.02	-15.96	13.09	16.49	3.41
7	27/12/2016	Panepane	-	F	46.52	-16.16	-16.13	13.74	16.35	3.39
8	29/12/2016	Pukahina Beach	-	F	44.29	-16.16	-15.97	12.50	16.69	3.54
9	30/12/2016	Papamoa Beach	291	F	49.65	-16.28	-16.21	14.53	16.56	3.42
10	2/01/2017	Papamoa Beach	278	F	50.25	-16.37	-16.32	14.76	16.43	3.40
11	2/01/2017	Papamoa Beach	302	F	50.06	-16.45	-16.44	14.85	16.69	3.37
12	5/01/2017	Panepane	278	F	50.11	-15.81	-15.81	14.93	16.61	3.36
13	5/01/2017	Panepane	301	F	48.67	-16.11	-16.09	14.42	16.93	3.38
14	7/01/2017	Papamoa Beach	248.5	F	50.93	-16.48	-16.44	15.01	16.70	3.39
15	12/01/2017	Lower Harbour	290	F	47.47	-16.60	-16.56	13.99	16.27	3.39
16	13/01/2017	Lower Harbour	289	F	49.59	-16.40	-16.38	14.73	16.01	3.37
17	15/01/2017	Papamoa Beach	286	M	50.93	-15.75	-15.77	15.26	18.42	3.34
18	23/01/2017	Papamoa Beach	287	F	48.81	-16.29	-16.33	14.72	16.54	3.32
19	23/01/2017	Papamoa Beach	287.5	F	47.84	-16.21	-16.19	14.16	16.47	3.38
20	24/01/2017	Papamoa Beach	-	F	30.73	-16.12	-15.92	8.65	16.42	3.55
21	29/01/2017	Papamoa Beach	305	F	50.46	-16.28	-16.26	14.95	16.55	3.38
22	5/02/2017	Panepane	290	F	41.93	-14.83	-14.61	11.70	16.38	3.58
23	5/02/2017	Panepane	293	M	50	-16.53	-16.51	14.84	16.23	3.37

Appendix 6 continued.

Shark	Date	Location	TL_{flex} (cm)	Sex	% C	$\delta^{13}C$	$\delta^{13}C$*	%N	$\delta^{15}N$	C:N
24	5/02/2017	Panepane	253	F	50.05	-16.90	-16.89	14.87	16.38	3.37
25	17/02/2017	Lower Harbour	294	F	50.37	-16.22	-16.17	14.79	16.53	3.41
26	24/02/2017	Papamoa Beach	272	F	50.37	-16.49	-16.46	14.86	16.79	3.39
27	27/02/2017	Papamoa Beach	293	F	50.94	-16.24	-16.24	15.20	16.93	3.35
28	27/02/2017	Papamoa Beach	291	F	50.04	-15.58	-15.58	14.91	15.88	3.36
29	27/02/2017	Papamoa Beach	305	F	50.59	-16.28	-16.27	15.04	16.76	3.36
30	28/02/2017	Papamoa Beach	297	F	50.39	-16.19	-16.19	15.04	16.57	3.35
31	28/02/2017	Papamoa Beach	287	F	48.47	-16.31	-16.28	14.35	17.09	3.38
32	17/03/2017	Lower Harbour	-	F	49.53	-16.00	-15.99	14.71	16.72	3.37
33	26/03/2017	Mount Beach	305	F	51.71	-16.17	-16.11	15.16	16.32	3.41
34	26/03/2017	Mount Beach	300	F	50.1	-16.55	-16.49	14.68	15.70	3.41
35	1/04/2017	Panepane	297	F	50.35	-16.18	-16.13	14.82	17.10	3.40
36	8/04/2017	Panepane	286.5	F	48.92	-16.29	-16.21	14.22	16.69	3.44
37	8/04/2017	Panepane	279	F	50.49	-16.10	-16.08	15.00	16.73	3.37
38	8/04/2017	Panepane	286.5	F	50.36	-16.04	-16.03	14.99	16.87	3.36
39**	6/05/2017	Panepane	-	F	49.82	-15.99	-15.95	14.70	16.69	3.39
40	21/05/2017	Panepane	282	F	51.75	-16.21	-16.21	15.45	16.55	3.35

*$\delta^{13}C$ post lipid correction

** indicates recapture of shark number 32

Appendix 7: Summary of capture and stable isotope data of coastal teleosts snapper (*Pagrus auratus*), kingfish (*Seriola lalandi*), kahawai (*Arripis trutta*), tarakihi (*Nemadactylus macropterus*) and piper (*Hyporhamphus ihi*) in the Bay of Plenty, New Zealand.

Species	Date	Location	FL (cm)*	%C	$\delta^{13}C$	$\delta^{13}C$**	%N	$\delta^{15}N$	C:N
Snapper	13/01/2017	Harbour	41	48.46	-17.74	-17.30	12.77	14.00	3.79
Snapper	21/01/2017	Papamoa Beach	36.5	49.20	-18.24	-17.77	12.85	14.64	3.83
Snapper	24/01/2017	Papamoa Beach	39.5	46.03	-16.54	-16.61	14.02	14.35	3.28
Snapper	28/01/2017	Matakana Island	30.5	47.09	-16.37	-16.43	14.33	15.48	3.29
Snapper	28/01/2017	Matakana Island	34	48.26	-17.07	-17.07	14.39	14.61	3.35
Snapper	25/02/2017	Papamoa Beach	34	47.16	-17.99	-18.02	14.17	14.46	3.33
Snapper	27/02/2017	Papamoa Beach	39	46.56	-17.58	-17.58	13.86	14.72	3.36
Snapper	27/02/2017	Papamoa Beach	38	46.17	-18.09	-18.14	13.97	13.88	3.30
Snapper	3/03/2017	Papamoa Beach	36.5	48.67	-17.25	-16.76	12.64	15.12	3.85
Snapper	2/04/2017	Rabbit Island	53	45.79	-16.35	-16.44	14.06	15.71	3.26
Kingfish	5/01/2017	Panepane	80	47.31	-14.58	-14.61	14.26	14.57	3.32
Kingfish	11/02/2017	Harbour	77	51.06	-15.71	-14.84	12.06	14.12	4.23
Kingfish	15/02/2017	Arataki Beach	112	46.29	-15.68	-15.69	13.86	15.45	3.34
Kingfish	3/03/2017	Leisure Island	90	48.17	-16.34	-16.41	14.69	15.38	3.28
Kingfish	4/03/2017	Motiti Island	110 est.	52.00	-18.61	-17.75	12.32	15.32	4.22
Kingfish	4/03/2017	Motiti Island	110 est.	44.65	-18.00	-18.01	13.37	14.40	3.34
Kingfish	4/03/2017	Motiti Island	110 est.	46.69	-16.55	-16.62	14.20	15.22	3.29
Kingfish	19/03/2017	Karewa Island	91.5	48.22	-16.91	-16.97	14.65	15.34	3.29
Kingfish	23/03/2017	Mount area	110est.	45.93	-14.86	-14.96	14.13	16.18	3.25
Kahawai	5/07/2017	Harbour		47.56	-17.05	-17.07	14.30	13.42	3.33
Kahawai	10/07/2017	Papamoa Beach		45.81	-17.79	-17.92	14.25	12.76	3.21
Kahawai	17/07/2017	Mount area	43.5	48.77	-17.33	-17.41	14.90	13.91	3.27
Kahawai	17/07/2017	Mount area	45.5	46.56	-18.01	-18.07	14.17	13.53	3.29

Appendix 7 continued.

Species	Date	Location	FL (cm)*	%C	$\delta^{13}C$	$\delta^{13}C$**	%N	$\delta^{15}N$	C:N
Kahawai	17/07/2017	Mount area	34.5	47.40	-17.92	-17.97	14.38	14.11	3.30
Kahawai	17/07/2017	Mount area	38	48.85	-17.65	-17.70	14.80	13.92	3.30
Kahawai	17/07/2017	Mount area	44.5	48.61	-17.79	-17.84	14.73	13.61	3.30
Kahawai	24/07/2017	Panepane	40 est.	47.22	-16.56	-16.65	14.47	13.89	3.26
Kahawai	2/08/2017	Kaituna Cut	51.5	47.75	-17.58	-17.65	14.54	13.17	3.28
Kahawai	2/08/2017	Kaituna Cut	47	49.15	-17.87	-17.97	15.10	13.86	3.25
Kahawai	18/07/2017	Harbour	17.5	46.85	-19.26	-19.32	14.25	11.84	3.29
Kahawai	18/07/2017	Harbour	16.5	47.96	-17.87	-17.91	14.49	11.96	3.31
Kahawai	18/07/2017	Harbour	15.5	48.85	-15.36	-15.39	14.69	12.83	3.33
Kahawai	18/07/2017	Harbour	16	48.81	-17.99	-18.02	14.66	12.12	3.33
Kahawai	24/07/2017	Panepane	26.5	46.83	-17.28	-17.37	14.34	13.53	3.27
Kahawai	25/07/2017	Harbour	17	48.43	-16.02	-16.07	14.66	12.31	3.30
Kahawai	25/07/2017	Harbour	17.5	47.43	-13.99	-14.02	14.30	12.57	3.32
Kahawai	6/08/2017	Panepane	26.5	48.62	-17.30	-17.39	14.89	13.97	3.27
Kahawai	6/08/2017	Panepane	25	47.18	-16.49	-16.57	14.43	13.88	3.27
Kahawai	6/08/2017	Panepane	16.5	46.51	-16.05	-16.12	14.17	13.64	3.28
Tarakihi	30/07/2017	Middle ground	35	46.65	-18.27	-18.35	14.27	13.73	3.27
Tarakihi	30/07/2017	Middle ground	33	48.68	-18.46	-18.29	13.80	15.48	3.53
Tarakihi	30/07/2017	Middle ground	33	46.63	-18.46	-18.51	14.14	14.28	3.30
Tarakihi	30/07/2017	Middle ground	32	47.51	-18.30	-18.35	14.40	14.86	3.30
Tarakihi	30/07/2017	Middle ground	30.5	47.58	-18.84	-18.86	14.29	14.32	3.33
Tarakihi	30/07/2017	Middle ground	34.5	47.79	-19.32	-19.39	14.60	13.48	3.27
Tarakihi	30/07/2017	Middle ground	34	46.62	-18.44	-18.52	14.25	13.95	3.27
Tarakihi	30/07/2017	Middle ground	39.5	46.59	-18.52	-18.62	14.30	14.47	3.26
Tarakihi	30/07/2017	Middle ground	31	47.04	-19.86	-19.91	14.24	13.46	3.30

Appendix 7 continued.

Species	Date	Location	FL (cm)*	%C	$\delta^{13}C$	$\delta^{13}C$**	%N	$\delta^{15}N$	C:N
Piper	3/09/2017	Harbour	26.5	45.28	-16.02	-16.13	13.98	12.63	3.24
Piper	3/09/2017	Harbour	29	45.75	-15.12	-15.27	14.33	12.68	3.19
Piper	3/09/2017	Harbour	28.5	45.31	-15.24	-15.43	14.33	12.59	3.16
Piper	3/09/2017	Harbour	26	44.51	-15.85	-16.07	14.23	13.06	3.13
Piper	3/09/2017	Harbour	28.5	45.02	-13.61	-13.82	14.32	12.37	3.14

*FL = Fork length

**$\delta^{13}C$ post lipid correction

est. = length of fish was estimated. Not measured.

Appendix 8: Summary of collection and stable isotope data of green-lipped mussels (*Perna canaliculus*) in the Bay of Plenty, New Zealand.

Species	Date	Location	%C	$\delta^{13}C$	$\delta^{13}C$*	%N	$\delta^{15}N$	C:N
Mussels	13/12/2016	Pilot Bay	42.65	-17.64	-17.61	12.58	8.75	3.39
Mussels	13/12/2016	Pilot Bay	46.28	-17.58	-17.53	13.61	8.41	3.40
Mussels	13/12/2016	Pilot Bay	43.06	-17.12	-17.19	13.09	9.22	3.29
Mussels	13/12/2016	Pilot Bay	46.12	-17.42	-17.49	14.01	8.38	3.29
Mussels	13/12/2016	Pilot Bay	42.75	-17.50	-17.47	12.64	8.50	3.38
Mussels	13/12/2016	Sulphur Point	44.06	-16.92	-17.00	13.48	9.45	3.27
Mussels	13/12/2016	Sulphur Point	44.61	-17.07	-17.05	13.21	9.90	3.38
Mussels	13/12/2016	Sulphur Point	44.25	-17.08	-17.13	13.39	9.11	3.30
Mussels	13/12/2016	Sulphur Point	44.21	-16.89	-16.90	13.22	9.12	3.34
Mussels	13/12/2016	Sulphur Point	43.97	-16.93	-16.93	13.13	9.26	3.35
Mussels	29/01/2017	Pilot Bay	44.34	-17.52	-17.57	13.43	8.47	3.30
Mussels	29/01/2017	Pilot Bay	43.96	-17.34	-17.43	13.45	9.30	3.27
Mussels	29/01/2017	Pilot Bay	43.54	-17.29	-17.34	13.21	8.87	3.30
Mussels	29/01/2017	Pilot Bay	44.11	-17.49	-17.51	13.23	8.96	3.33
Mussels	29/01/2017	Pilot Bay	44.43	-17.44	-17.52	13.60	8.75	3.27
Mussels	27/01/2017	Sulphur Point	43.94	-16.91	-17.00	13.46	9.05	3.26
Mussels	27/01/2017	Sulphur Point	44.69	-17.18	-17.20	13.43	9.12	3.33
Mussels	27/01/2017	Sulphur Point	44.61	-17.07	-17.08	13.33	9.08	3.35
Mussels	27/01/2017	Sulphur Point	44.60	-17.07	-17.12	13.51	9.05	3.30
Mussels	27/01/2017	Sulphur Point	47.15	-17.09	-17.15	14.34	9.02	3.29
Mussels	30/01/2017	Shark Alley	44.09	-17.78	-17.71	12.89	7.76	3.42
Mussels	30/01/2017	Shark Alley	44.26	-17.73	-17.75	13.30	8.28	3.33
Mussels	30/01/2017	Shark Alley	39.00	-17.17	-17.06	11.26	7.83	3.46
Mussels	30/01/2017	Shark Alley	43.99	-17.68	-17.63	12.93	7.85	3.40
Mussels	30/01/2017	Shark Alley	43.59	-17.66	-17.66	13.00	8.31	3.35
Mussels	5/02/2017	Mount	43.44	-17.40	-17.43	13.07	9.03	3.32
Mussels	5/02/2017	Mount	44.04	-17.48	-17.53	13.34	8.80	3.30
Mussels	5/02/2017	Mount	44.30	-17.46	-17.52	13.49	9.04	3.28
Mussels	5/02/2017	Mount	43.73	-17.49	-17.57	13.37	8.81	3.27
Mussels	5/02/2017	Mount	44.07	-17.39	-17.51	13.60	9.18	3.24
Mussels	7/03/2017	Pilot Bay	44.41	-17.12	-17.17	13.44	9.54	3.30
Mussels	7/03/2017	Pilot Bay	43.55	-17.42	-17.34	12.70	8.63	3.43
Mussels	7/03/2017	Pilot Bay	44.11	-17.16	-17.26	13.57	8.69	3.25
Mussels	7/03/2017	Pilot Bay	45.03	-17.02	-17.11	13.78	9.31	3.27
Mussels	7/03/2017	Pilot Bay	44.11	-17.10	-17.20	13.59	8.95	3.25
Mussels	11/03/2017	Sulphur Point	45.21	-16.83	-16.94	13.93	9.33	3.25
Mussels	11/03/2017	Sulphur Point	46.55	-17.03	-17.13	14.35	9.53	3.24
Mussels	11/03/2017	Sulphur Point	44.67	-16.72	-16.79	13.61	9.95	3.28
Mussels	11/03/2017	Sulphur Point	44.88	-16.76	-16.86	13.78	9.90	3.26
Mussels	11/03/2017	Sulphur Point	45.86	-16.83	-16.98	14.31	9.56	3.20

Appendix 8 continued.

Species	Date	Location	%C	$\delta^{13}C$	$\delta^{13}C$*	%N	$\delta^{15}N$	C:N
Mussels	17/03/2017	Shark Alley	44.58	-17.51	-17.62	13.75	8.07	3.24
Mussels	17/03/2017	Shark Alley	44.61	-17.27	-17.40	13.83	9.22	3.23
Mussels	17/03/2017	Shark Alley	44.77	-17.24	-17.33	13.73	8.10	3.26
Mussels	17/03/2017	Shark Alley	44.31	-17.40	-17.50	13.63	8.56	3.25
Mussels	17/03/2017	Shark Alley	45.12	-17.50	-17.58	13.80	8.53	3.27
Mussels	17/03/2017	Mount	44.72	-17.66	-17.73	13.64	8.60	3.28
Mussels	17/03/2017	Mount	44.52	-17.35	-17.44	13.64	8.94	3.26
Mussels	17/03/2017	Mount	44.15	-17.27	-17.32	13.38	9.26	3.30
Mussels	17/03/2017	Mount	44.19	-17.34	-17.35	13.22	9.32	3.34
Mussels	17/03/2017	Mount	44.37	-17.35	-17.39	13.39	8.81	3.31
Mussels	6/05/2017	Pilot Bay	44.25	-17.32	-17.37	13.42	8.99	3.30
Mussels	6/05/2017	Pilot Bay	44.71	-17.20	-17.23	13.47	8.89	3.32
Mussels	6/05/2017	Pilot Bay	44.18	-17.29	-17.32	13.31	9.03	3.32
Mussels	6/05/2017	Pilot Bay	44.31	-17.35	-17.43	13.51	8.83	3.28
Mussels	6/05/2017	Pilot Bay	44.91	-17.10	-17.18	13.71	9.09	3.28
Mussels	9/05/2017	Sulphur Point	45.19	-16.73	-16.90	14.19	9.66	3.18
Mussels	9/05/2017	Sulphur Point	45.27	-16.63	-16.78	14.11	9.57	3.21
Mussels	9/05/2017	Sulphur Point	44.41	-16.85	-16.99	13.81	9.49	3.22
Mussels	9/05/2017	Sulphur Point	44.33	-16.79	-16.90	13.70	9.31	3.24
Mussels	9/05/2017	Sulphur Point	43.89	-16.57	-16.70	13.58	9.76	3.23
Mussels	7/05/2017	Shark Alley	44.05	-17.62	-17.65	13.23	8.78	3.33
Mussels	7/05/2017	Shark Alley	44.88	-17.12	-17.19	13.68	9.63	3.28
Mussels	7/05/2017	Shark Alley	44.55	-17.34	-17.45	13.72	9.57	3.25
Mussels	7/05/2017	Shark Alley	44.03	-17.24	-17.26	13.20	9.67	3.34
Mussels	7/05/2017	Shark Alley	43.88	-17.33	-17.34	13.12	8.42	3.34
Mussels	7/05/2017	Mount	45.01	-17.65	-17.69	13.60	8.61	3.31
Mussels	7/05/2017	Mount	44.96	-17.37	-17.41	13.57	8.55	3.31
Mussels	7/05/2017	Mount	44.63	-17.51	-17.56	13.49	9.27	3.31
Mussels	7/05/2017	Mount	44.20	-17.52	-17.57	13.36	8.90	3.31
Mussels	7/05/2017	Mount	43.82	-17.57	-17.58	13.13	9.18	3.34

*$\delta^{13}C$ post lipid correction

Appendix 9: Summary of collection and stable isotope data of kelp (*Ecklonia radiata*) and seagrass (*Zostera marina*) in the Bay of Plenty, New Zealand.

Species	Date	Location	%C	$\delta^{13}C$	%N	$\delta^{15}N$	C:N
Zostera	26/08/2017	Fergusson Park	40.79	-9.98	2.52	4.83	16.21
Zostera	26/08/2017	Fergusson Park	40.86	-11.94	2.72	4.11	15.04
Zostera	26/08/2017	Fergusson Park	40.88	-9.72	2.40	4.03	17.05
Zostera	26/08/2017	Fergusson Park	40.43	-10.32	2.28	4.38	17.76
Zostera	26/08/2017	Fergusson Park	40.42	-10.83	2.68	3.89	15.10
Zostera	26/08/2017	Kulim Park	40.79	-9.81	2.30	5.45	17.75
Zostera	26/08/2017	Kulim Park	41.18	-10.52	2.18	4.31	18.88
Zostera	26/08/2017	Kulim Park	41.07	-10.03	2.23	4.57	18.38
Zostera	26/08/2017	Kulim Park	39.57	-9.47	1.94	4.27	20.35
Zostera	26/08/2017	Kulim Park	40.78	-9.85	2.19	5.49	18.60
Ecklonia	8/09/2017	Pilot Bay	38.50	-16.85	2.86	6.85	13.44
Ecklonia	8/09/2017	Pilot Bay	39.04	-14.62	2.63	6.63	14.87
Ecklonia	8/09/2017	Pilot Bay	39.44	-15.15	2.71	6.82	14.56
Ecklonia	8/09/2017	Pilot Bay	38.51	-15.48	2.38	6.92	16.19
Ecklonia	8/09/2017	Pilot Bay	38.26	-15.20	2.51	6.64	15.26
Ecklonia	14/09/2017	Rabbit Island	36.63	-20.52	1.86	4.65	19.67
Ecklonia	15/09/2017	Rabbit Island	38.57	-18.47	2.31	5.30	16.68
Ecklonia	16/09/2017	Rabbit Island	36.37	-20.66	2.00	4.63	18.22
Ecklonia	17/09/2017	Rabbit Island	36.57	-21.50	2.02	4.09	18.10
Ecklonia	18/09/2017	Rabbit Island	36.40	-21.24	1.88	3.90	19.37

Appendix 10: Summary of stable isotope data of pelagic teleosts jack mackerel (*Trachurus declivis*) and blue mackerel (*Scomber australasicus*) supplied by PELCO commercial fisheries in the Bay of Plenty, New Zealand.

Species	%C	$\delta^{13}C$	$\delta^{13}C$*	%N	$\delta^{15}N$	C:N
Jack mackerel	48.40	-19.79	-19.08	11.88	12.57	4.07
Jack mackerel	53.40	-20.69	-19.29	11.19	11.44	4.77
Jack mackerel	48.50	-19.72	-19.12	12.27	11.72	3.95
Jack mackerel	53.90	-20.45	-19.12	11.48	12.87	4.70
Jack mackerel	53.46	-20.25	-19.06	11.74	12.67	4.55
Jack mackerel	48.27	-18.65	-18.50	13.77	12.41	3.51
Jack mackerel	53.52	-20.23	-19.05	11.77	13.06	4.55
Jack mackerel	50.90	-19.50	-18.78	12.49	12.78	4.08
Jack mackerel	45.17	-18.29	-18.33	13.64	12.89	3.31
Jack mackerel	49.99	-19.58	-19.07	12.94	12.45	3.86
Jack mackerel	48.82	-20.17	-19.66	12.60	11.32	3.87
Jack mackerel	46.80	-18.14	-18.22	14.31	12.44	3.27
Jack mackerel	48.41	-18.72	-18.53	13.65	12.67	3.55
Jack mackerel	52.45	-20.65	-19.53	11.69	12.14	4.49
Jack mackerel	52.79	-20.86	-19.71	11.69	11.87	4.52
Blue mackerel	47.55	-19.00	-18.93	13.89	11.65	3.42
Blue mackerel	50.73	-20.03	-19.56	13.25	11.93	3.83
Blue mackerel	50.34	-19.55	-19.26	13.79	11.61	3.65
Blue mackerel	47.70	-19.35	-19.29	13.96	11.67	3.42
Blue mackerel	47.20	-18.82	-18.91	14.49	11.57	3.26
Blue mackerel	50.49	-20.14	-19.50	12.63	11.60	4.00
Blue mackerel	46.97	-19.13	-19.19	14.26	11.84	3.29
Blue mackerel	48.31	-19.32	-19.24	14.05	11.48	3.44
Blue mackerel	51.93	-20.41	-19.66	12.63	11.72	4.11
Blue mackerel	47.09	-19.16	-19.11	13.84	11.86	3.40
Blue mackerel	47.35	-19.08	-19.13	14.33	11.59	3.30
Blue mackerel	46.45	-19.00	-19.04	14.04	11.89	3.31
Blue mackerel	48.63	-19.64	-19.35	13.34	11.74	3.65
Blue mackerel	46.91	-19.06	-19.08	14.09	11.58	3.33
Blue mackerel	48.78	-19.21	-19.09	14.04	12.19	3.47

*$\delta^{13}C$ post lipid correction

Appendix 11: Summary of field and stable isotope data supplied by Huteau (2015) of mud whelk (*Cominella glandiformis*), mud snails (*Amphibola crenata*), cockle (*Austrovenus stutchburyi*), oysters (*Magallana gigas*), sea lettuce (*Ulva lactuca*), mangroves (*Avicennia marina var. australasica*), seagrass (*Zostera marina*) and surface sediment collected from estuarine areas within the Bay of Plenty, New Zealand.

Data	Species	Location	%C	$\delta^{13}C$	$\delta^{13}C$*	%N	$\delta^{15}N$	C:N
Huteau	Surface sediment	Rangataua	0.76	-20.01		0.30	5.51	2.58
Huteau	Surface sediment	Rangataua	0.13	-15.82		0.25	5.14	0.53
Huteau	Surface sediment	Rangataua	0.16	-15.31		0.11	6.62	1.47
Huteau	Surface sediment	Rangataua	0.33	-19.10		0.03	6.21	12.74
Huteau	Surface sediment	Rangataua	0.41	-18.01		0.04	5.38	9.43
Huteau	Surface sediment	Rangataua	0.36	-15.74		0.06	8.33	6.04
Huteau	Surface sediment	Rangataua	0.73	-20.66		0.07	8.47	11.05
Huteau	Surface sediment	Rangataua	3.44	-25.88		0.06	5.93	55.49
Huteau	Surface sediment	Rangataua	2.99	-24.05		0.28	4.38	10.82
Huteau	Surface sediment	Rangataua	3.24	-23.46		0.10	5.61	33.70
Huteau	Surface sediment	Waimapu	4.06	-27.33		0.21	4.27	19.23
Huteau	Surface sediment	Waimapu	7.03	-27.17		0.61	5.03	11.46
Huteau	Surface sediment	Waimapu	6.92	-37.96		0.61	5.32	11.26
Huteau	Surface sediment	Waimapu	4.66	-26.59		0.35	4.72	13.43
Huteau	Surface sediment	Waimapu	3.68	-24.87		0.30	4.89	12.08
Huteau	Surface sediment	Waimapu	1.20	-22.58		0.11	5.26	11.35
Huteau	Surface sediment	Waimapu	1.61	-22.87		0.13	5.88	12.21
Huteau	Surface sediment	Waimapu	0.73	-21.43		0.09	5.97	7.97
Huteau	Surface sediment	Waimapu	1.98	-18.03		0.17	5.52	11.58
Huteau	Surface sediment	Waikareao	1.67	-26.22		0.12	4.48	13.66

Appendix 11 continued.

Data	Species	Location	%C	$\delta^{13}C$	$\delta^{13}C$*	%N	$\delta^{15}N$	C:N
Huteau	Surface sediment	Waikareao	2.23	-26.28		0.17	4.19	13.51
Huteau	Surface sediment	Waikareao	1.42	-21.80		0.12	5.29	11.38
Huteau	Surface sediment	Waikareao	0.36	-18.96		0.05	4.12	8.08
Huteau	Surface sediment	Waikareao	0.40	-18.59		0.07	6.99	5.83
Huteau	Surface sediment	Waikareao	0.25	-20.00		0.04	5.96	6.59
Huteau	Surface sediment	Waikareao	5.56	-26.60		0.27	4.42	20.96
Huteau	Surface sediment	Waikareao	5.62	-26.31		0.28	4.49	19.81
Huteau	Surface sediment	Ohiwa	0.92	-23.61		0.03	6.72	35.74
Huteau	Surface sediment	Ohiwa	1.05	-24.46		0.10	4.41	10.07
Huteau	Surface sediment	Ohiwa	0.45	-23.54		0.05	3.98	8.18
Huteau	Surface sediment	Ohiwa	0.81	-25.46		0.06	2.86	12.88
Huteau	Surface sediment	Tuapiro	1.41	-21.01		0.18	5.35	8.02
Huteau	Surface sediment	Tuapiro	1.05	-22.55		0.09	3.96	11.65
Huteau	Surface sediment	Waikareao	3.04	-26.91		0.26	3.29	11.83
Huteau	Surface sediment	Waikareao	3.24	-25.97		0.26	3.42	12.64
Huteau	Surface sediment	Waikareao	0.91	-24.15		0.10	5.87	9.24
Huteau	Surface sediment	Waikareao	0.26	-17.97		0.06	6.60	4.44
Huteau	Surface sediment	Waikareao	0.26	-19.50		0.04	6.59	5.78
Huteau	Surface sediment	Rangataua	1.94	-23.47		0.27	5.94	7.16
Huteau	Surface sediment	Rangataua	0.30	-20.56		0.09	7.42	3.44
Huteau	Surface sediment	Rangataua	0.38	-18.73		0.06	6.80	6.30
Huteau	Surface sediment	Waimapu	0.84	-24.02		0.10	3.44	8.19
Huteau	Surface sediment	Waimapu	0.99	-24.90		0.15	5.55	6.43
Huteau	Surface sediment	Waimapu	5.77	-26.98		0.60	4.43	9.62
Huteau	Surface sediment	Waimapu	0.19	-18.66		0.05	7.49	4.07

Appendix 11 continued.

Data	Species	Location	%C	$\delta^{13}C$	$\delta^{13}C$*	%N	$\delta^{15}N$	C:N
Huteau	Mangrove	Rangataua	45.57	-26.37		2.60	7.47	17.50
Huteau	Mangrove	Rangataua	45.28	-26.53		2.75	4.05	16.49
Huteau	Mangrove	Rangataua	45.26	-26.95		2.83	5.90	16.01
Huteau	Mangrove	Rangataua	44.16	-26.05		2.87	7.73	15.39
Huteau	Mangrove	Waimapu	47.15	-25.42		1.90	6.69	24.87
Huteau	Mangrove	Waimapu	45.63	-25.68		2.17	7.29	21.00
Huteau	Mangrove	Waimapu	41.98	-26.06		3.03	7.95	13.85
Huteau	Mangrove	Waikareao	40.59	-27.82		3.75	5.63	10.83
Huteau	Mangrove	Waikareao	45.37	-27.93		2.81	7.56	16.12
Huteau	Mangrove	Waikareao	44.10	-25.66		3.30	9.34	13.37
Huteau	Mangrove	Waikareao	42.47	-28.19		3.47	6.34	12.23
Huteau	Mangrove	Ohiwa	45.89	-25.78		2.53	5.45	18.13
Huteau	Mangrove	Tuapiro	60.69	-28.58		11.20	-3.78	5.42
Huteau	Mangrove	Waikareao	41.85	-25.67		2.42	7.60	17.31
Huteau	Mangrove	Waikareao	41.19	-25.08		1.70	8.97	24.19
Huteau	Mangrove	Waikareao	40.31	-26.64		2.09	6.20	19.24
Huteau	Mangrove	Rangataua	39.42	-26.97		1.92	6.62	20.53
Huteau	Mangrove	Rangataua	42.49	-25.39		2.45	12.52	17.34
Huteau	Mangrove	Waimapu	42.46	-25.16		2.23	6.41	19.07
Huteau	Mangrove	Waimapu	43.05	-25.84		2.12	5.70	20.31
Huteau	Zostera	Rangataua	36.71	-13.10		2.41	7.81	15.20
Huteau	Zostera	Rangataua	38.20	-19.29		2.89	7.60	13.23
Huteau	Zostera	Rangataua	38.90	-19.94		3.21	7.22	12.11
Huteau	Zostera	Waimapu	41.21	-25.78		3.22	3.18	12.80
Huteau	Zostera	Waimapu	42.35	-32.12		3.47	6.12	12.21

Appendix 11 continued.

Data	Species	Location	%C	$\delta^{13}C$	$\delta^{13}C$*	%N	$\delta^{15}N$	C:N
Huteau	Zostera	Waimapu	40.74	-15.54		3.40	6.75	11.99
Huteau	Zostera	Waimapu	41.53	-18.01		2.52	6.82	16.49
Huteau	Zostera	Waimapu	40.58	-12.70		3.33	6.84	12.19
Huteau	Zostera	Waikareao	39.34	-23.06		3.19	2.44	12.35
Huteau	Zostera	Waikareao	40.73	-20.95		3.36	6.04	12.14
Huteau	Zostera	Waikareao	38.84	-10.92		2.82	5.18	13.77
Huteau	Zostera	Waikareao	40.37	-26.81		2.70	5.09	14.97
Huteau	Zostera	Tuapiro	41.56	-12.01		2.93	5.30	14.16
Huteau	Zostera	Tuapiro	35.80	-11.33		1.73	6.00	20.73
Huteau	Zostera	Waikareao	32.89	-22.07		2.62	-1.06	12.57
Huteau	Zostera	Waikareao	29.90	-13.90		1.74	8.71	17.19
Huteau	Zostera	Waikareao	36.96	-10.35		2.49	4.30	14.83
Huteau	Zostera	Rangataua	34.64	-10.15		2.22	7.37	15.63
Huteau	Zostera	Waimapu	36.14	-19.16		2.40	6.56	15.09
Huteau	Zostera	Waimapu	36.44	-15.69		2.69	5.80	13.55
Huteau	Zostera	Waimapu	37.13	-11.58		2.95	7.21	12.60
Huteau	Ulva	Rangataua	32.30	-10.84		2.77	8.25	11.67
Huteau	Ulva	Rangataua	35.16	-14.28		3.06	9.13	11.48
Huteau	Ulva	Rangataua	31.89	-12.32		2.83	9.11	11.26
Huteau	Ulva	Rangataua	36.83	-14.41		3.44	9.02	10.72
Huteau	Ulva	Waimapu	37.03	-11.11		3.79	7.62	9.76
Huteau	Ulva	Waimapu	37.44	-12.62		2.98	7.46	12.58
Huteau	Ulva	Waimapu	35.08	-10.92		3.19	6.71	10.99
Huteau	Ulva	Waikareao	35.79	-15.24		3.88	7.06	9.21
Huteau	Ulva	Waikareao	34.69	-12.56		3.43	7.04	10.10

Appendix 11 continued.

Data	Species	Location	%C	$\delta^{13}C$	$\delta^{13}C$*	%N	$\delta^{15}N$	C:N
Huteau	Ulva	Waikareao	27.79	-14.67		2.22	7.05	12.55
Huteau	Ulva	Waikareao	29.22	-14.82		2.74	6.80	10.66
Huteau	Ulva	Tuapiro	34.60	-14.84		2.44	7.71	14.16
Huteau	Ulva	Waikareao	30.70	-13.74		2.49	7.24	12.34
Huteau	Ulva	Rangataua	31.76	-11.25		2.87	9.79	11.07
Huteau	Mudsnail	Rangataua	16.61	-15.94	-14.80	3.69	8.46	4.50
Huteau	Mudsnail	Rangataua	26.54	-9.95	-8.92	6.04	10.35	4.39
Huteau	Mudsnail	Rangataua	27.96	-10.74	-9.67	6.31	9.34	4.43
Huteau	Mudsnail	Rangataua	26.67	-13.48	-12.23	5.78	8.41	4.61
Huteau	Mudsnail	Rangataua	25.49	-17.39	-16.92	6.66	7.80	3.83
Huteau	Mudsnail	Waimapu	36.36	-13.83	-13.00	8.67	9.20	4.20
Huteau	Mudsnail	Waimapu	29.36	-11.94	-10.29	5.84	8.52	5.02
Huteau	Mudsnail	Waimapu	34.38	-12.57	-11.99	8.73	9.18	3.94
Huteau	Mudsnail	Waimapu	21.58	-10.36	-9.43	5.03	8.16	4.29
Huteau	Mudsnail	Waikareao	33.32	-15.56	-14.87	8.24	8.75	4.05
Huteau	Mudsnail	Tuapiro	34.10	-13.14	-12.46	8.45	7.51	4.04
Huteau	Mudsnail	Tuapiro	30.05	-16.14	-14.20	5.65	5.80	5.32
Huteau	Mudsnail	Waikareao	34.94	-18.21	-17.75	9.14	7.99	3.82
Huteau	Mudsnail	Rangataua	37.43	-18.26	-17.80	9.80	8.03	3.82
Huteau	Mudsnail	Rangataua	22.57	-12.33	-12.04	6.19	8.64	3.65
Huteau	Mudsnail	Rangataua	17.60	-11.74	-11.44	4.81	8.82	3.66
Huteau	Mudsnail	Rangataua	32.58	-19.32	-18.93	8.70	7.63	3.74
Huteau	Mudsnail	Rangataua	23.05	-12.11	-11.70	6.12	12.08	3.77
Huteau	Mudsnail	Waimapu	40.90	-14.09	-13.50	10.36	8.90	3.95
Huteau	Mudsnail	Waimapu	35.79	-13.54	-13.34	10.08	7.87	3.55

Appendix 11 continued.

Data	Species	Location	%C	$\delta^{13}C$	$\delta^{13}C$*	%N	$\delta^{15}N$	C:N
Huteau	Mudsnail	Waimapu	28.77	-12.45	-12.04	7.64	8.60	3.76
Huteau	Mudsnail	Waimapu	29.29	-12.59	-12.05	7.52	8.23	3.89
Huteau	Cockle	Waikareao	33.56	-16.73	-15.93	8.06	8.05	4.17
Huteau	Cockle	Waikareao	34.51	-17.44	-16.56	8.13	7.78	4.24
Huteau	Cockle	Waikareao	32.03	-18.20	-17.30	7.53	8.18	4.26
Huteau	Cockle	Waikareao	38.25	-18.36	-17.50	9.05	8.24	4.23
Huteau	Cockle	Waikareao	35.14	-18.28	-17.40	8.29	8.21	4.24
Huteau	Cockle	Rangataua	34.80	-19.92	-18.82	7.80	8.06	4.46
Huteau	Cockle	Waimapu	37.55	-19.55	-18.67	8.86	7.11	4.24
Huteau	Cockle	Ohiwa	37.03	-18.85	-18.08	8.97	8.25	4.13
Huteau	Cockle	Ohiwa	33.00	-19.45	-18.52	7.68	7.88	4.30
Huteau	Cockle	Rangataua	37.13	-18.97	-18.25	9.11	8.22	4.08
Huteau	Cockle	Rangataua	37.21	-18.16	-17.47	9.18	8.40	4.06
Huteau	Cockle	Tuapiro	33.06	-18.61	-17.75	7.84	7.89	4.22
Huteau	Cockle	Waimapu	34.26	-19.16	-18.53	8.59	7.84	3.99
Huteau	Oyster	Waikareao	35.24	-22.37	-20.81	7.15	5.45	4.93
Huteau	Oyster	Waikareao	42.20	-20.67	-18.63	7.79	5.02	5.42
Huteau	Oyster	Waikareao	38.15	-19.37	-18.15	8.33	7.78	4.58
Huteau	Oyster	Waikareao	42.36	-22.51	-21.14	8.94	5.62	4.74
Huteau	Oyster	Waikareao	41.81	-20.62	-19.17	8.67	6.40	4.82
Huteau	Oyster	Waikareao	40.67	-19.20	-18.06	9.03	8.24	4.50
Huteau	Oyster	Waikareao	43.67	-19.48	-17.62	8.34	7.35	5.24
Huteau	Oyster	Ohiwa	40.46	-19.92	-18.42	8.31	7.83	4.87
Huteau	Oyster	Ohiwa	40.74	-25.29	-22.49	6.59	6.09	6.18
Huteau	Oyster	Tuapiro	40.46	-19.50	-18.43	9.12	7.44	4.44

Appendix 11 continued.

Data	Species	Location	%C	$\delta^{13}C$	$\delta^{13}C$*	%N	$\delta^{15}N$	C:N
Huteau	Oyster	Tuapiro	40.06	-20.82	-19.40	8.36	6.97	4.79
Huteau	Oyster	Waimapu	42.11	-20.67	-19.95	10.31	7.94	4.09
Huteau	Mudwhelk	Waikareao	35.80	-15.39	-14.46	8.34	11.45	4.30
Huteau	Mudwhelk	Rangataua	40.21	-10.40	-9.70	9.91	12.59	4.06
Huteau	Mudwhelk	Waimapu	40.16	-11.29	-10.59	9.89	11.86	4.06

*$\delta^{13}C$ post lipid correction

Appendix 12: Summary of field and stable isotope data supplied by McCormack (2021) of sponges (*Stellatta crater*) collected from Motunau (Plate) Island, Bay of Plenty, New Zealand.

Data	Species	Location	%C	$\delta^{13}C$	%N	$\delta^{15}N$	C:N
McCormack	Sponge	Plate Island	12.29	-20.63	2.76	10.26	4.45
McCormack	Sponge	Plate Island	12.27	-20.63	2.80	10.40	4.38
McCormack	Sponge	Plate Island	12.36	-20.66	2.80	10.27	4.41
McCormack	Sponge	Plate Island	13.50	-20.72	3.02	10.26	4.47
McCormack	Sponge	Plate Island	13.51	-20.69	3.05	10.12	4.43
McCormack	Sponge	Plate Island	13.47	-20.67	3.00	10.12	4.49

Appendix 13: Descriptive statistics for one-way ANOVA testing if shark length was a factor of month of capture.

	Nov Dec	Jan	Feb	Mar Apr
Mean	271	268.5555556	287.5555556	277.2222222
Standard Error	7.590198358	15.58164974	5.201792189	9.456813795
Median	275	287	293	286.5
Mode	251	#N/A	293	286.5
Standard Deviation	22.77059507	46.74494922	15.60537657	28.37044139
Sample Variance	518.5	2185.090278	243.5277778	804.8819444
Kurtosis	-1.33012921	6.623700996	2.603611287	0.170027696
Skewness	-0.11140302	-2.52164512	-1.61670676	-1.23385891
Range	66	151	52	77
Minimum	236	150	253	228
Maximum	302	301	305	305
Sum	2439	2417	2588	2495
Count	9	9	9	9

Appendix 13 continued.

SUMMARY

Groups	Count	Sum	Average	Variance
1	5	1317	263.4	512.3
2	5	1400	280	363.5
3	5	1457.5	291.5	59.25
4	5	1405	281	330.5
5	5	1494	298.8	55.2
6	5	1431	286.2	46.575

ANOVA

Source of Variation	SS	df	MS	F	P-value	F crit
Between Groups	3639.442	5	727.8883	3.194069	0.023783	2.620654
Within Groups	5469.3	24	227.8875			
Total	9108.742	29				

Appendix 14: Descriptive statistics for one-way ANOVA testing if shark length was a factor of location of capture.

	Upper Harbour	Panepane	Papamoa Beach	Lower Harbour	Mount Beach
Mean	263.4	277.3333	278.666667	275.25	302.5
Standard Error	10.12225271	6.141122	9.89416214	15.7869936	2.5
Median	260	284.25	287.5	289.5	302.5
Mode	#N/A	286.5	291	#N/A	#N/A
Standard Deviation	22.63404515	21.27347	38.3199252	31.5739872	3.535533906
Sample Variance	512.3	452.5606	1468.41667	996.916667	12.5
Kurtosis	-0.366941614	0.585991	10.3160887	3.91056489	#DIV/0!
Skewness	0.380848602	-1.17559	-3.06635204	-1.9715815	#DIV/0!
Range	59	70	155	66	5
Minimum	236	231	150	228	300
Maximum	295	301	305	294	305
Sum	1317	3328	4180	1101	605
Count	5	12	15	4	2
Largest(1)	295	301	305	294	305
Smallest(1)	236	231	150	228	300
Confidence Level(95.0%)	28.103879	13.51652	21.2208672	50.2412594	31.76551184

SUMMARY

Groups	*Count*	*Sum*	*Average*	*Variance*
1	4	1081	270.25	370.25
2	4	1162	290.5	91
3	4	1114.5	278.625	502.8958
4	4	1101	275.25	996.9167

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	890.1719	3	296.724	0.605231	0.624104	3.490295
Within Groups	5883.188	12	490.2656			
Total	6773.359	15				

Appendix 15: Description of paired t-tests to test for significant differences in $\delta^{13}C$ values of tissues pre- and post-mathematical lipid correction.

BRONZE WHALER SHARKS

	Variable 1	*Variable 2*
Mean	-16.1621645	-16.1221686
Variance	0.116217971	0.133588053
Observations	40	40
Pearson Correlation	0.990445532	
Hypothesized Mean Difference	0	
df	39	
t Stat	-4.62943682	
P(T<=t) one-tail	2.00089E-05	
t Critical one-tail	1.684875122	
P(T<=t) two-tail	4.00179E-05	
t Critical two-tail	2.02269092	

SNAPPER

	Variable 1	*Variable 2*
Mean	-17.3226213	-17.2126
Variance	0.519862844	0.41684
Observations	10	10
Pearson Correlation	0.939893399	
Hypothesized Mean Difference	0	
df	9	
t Stat	-1.400779871	
P(T<=t) one-tail	0.097401365	
t Critical one-tail	1.833112933	
P(T<=t) two-tail	0.19480273	
t Critical two-tail	2.262157163	

KINGFISH

	Variable 1	*Variable 2*
Mean	-16.3602207	-16.2085
Variance	1.800582795	1.582606
Observations	9	9
Pearson Correlation	0.953394838	
Hypothesized Mean Difference	0	
df	8	
t Stat	-1.12241746	
P(T<=t) one-tail	0.147119774	
t Critical one-tail	1.859548038	
P(T<=t) two-tail	0.294239548	
t Critical two-tail	2.306004135	

Appendix 15 continued.

KAHAWAI

	Variable 1	*Variable 2*
Mean	-17.1573268	-17.222479
Variance	1.333395491	1.35073947
Observations	20	20
Pearson Correlation	0.999729353	
Hypothesized Mean Difference	0	
df	19	
t Stat	10.41625173	
P(T<=t) one-tail	1.35886E-09	
t Critical one-tail	1.729132812	
P(T<=t) two-tail	2.71771E-09	
t Critical two-tail	2.093024054	

TARAKIHI

	Variable 1	*Variable 2*
Mean	-18.71870911	-18.7575
Variance	0.287742291	0.303254
Observations	9	9
Pearson Correlation	0.988931467	
Hypothesized Mean Difference	0	
df	8	
t Stat	1.415663876	
P(T<=t) one-tail	0.097302488	
t Critical one-tail	1.859548038	
P(T<=t) two-tail	0.194604975	
t Critical two-tail	2.306004135	

PIPER

	Variable 1	*Variable 2*
Mean	-15.1669664	-15.3457
Variance	0.902112079	0.869884
Observations	5	5
Pearson Correlation	0.999095612	
Hypothesized Mean Difference	0	
df	4	
t Stat	9.178051772	
P(T<=t) one-tail	0.000391297	
t Critical one-tail	2.131846786	
P(T<=t) two-tail	0.000782595	
t Critical two-tail	2.776445105	

Appendix 15 continued.

GREEN-LIPPED MUSSELS

	Variable 1	*Variable 2*
Mean	-17.25377791	-17.30762
Variance	0.082889524	0.0704212
Observations	70	70
Pearson Correlation	0.983715716	
Hypothesized Mean Difference	0	
df	69	
t Stat	8.230247833	
P(T<=t) one-tail	3.79002E-12	
t Critical one-tail	1.667238549	
P(T<=t) two-tail	7.58004E-12	
t Critical two-tail	1.994945415	

JACK MACKEREL

	Variable 1	*Variable 2*
Mean	-19.71213887	-19.003202
Variance	0.795711197	0.208102
Observations	15	15
Pearson Correlation	0.92203891	
Hypothesized Mean Difference	0	
df	14	
t Stat	-5.454335563	
P(T<=t) one-tail	4.24492E-05	
t Critical one-tail	1.761310136	
P(T<=t) two-tail	8.48983E-05	
t Critical two-tail	2.144786688	

BLUE MACKEREL

	Variable 1	*Variable 2*
Mean	-19.3942176	-19.2239697
Variance	0.221129871	0.04835393
Observations	15	15
Pearson Correlation	0.965880638	
Hypothesized Mean Difference	0	
df	14	
t Stat	-2.49697764	
P(T<=t) one-tail	0.01280789	
t Critical one-tail	1.761310136	
P(T<=t) two-tail	0.025615781	
t Critical two-tail	2.144786688	

Appendix 15 continued.

MUD WHELK

	Variable 1	*Variable 2*
Mean	-12.36141582	-11.584671
Variance	7.096575825	6.4060091
Observations	3	3
Pearson Correlation	0.999966162	
Hypothesized Mean Difference	0	
df	2	
t Stat	-9.992596452	
P(T<=t) one-tail	0.004933423	
t Critical one-tail	2.91998558	
P(T<=t) two-tail	0.009866846	
t Critical two-tail	4.30265273	

MUD SNAILS

	Variable 1	*Variable 2*
Mean	-13.89365437	-13.1537
Variance	7.13484053	7.650152
Observations	22	22
Pearson Correlation	0.986749652	
Hypothesized Mean Difference	0	
df	21	
t Stat	-7.669761152	
P(T<=t) one-tail	8.03956E-08	
t Critical one-tail	1.720742903	
P(T<=t) two-tail	1.60791E-07	
t Critical two-tail	2.079613845	

COCKLE

	Variable 1	*Variable 2*
Mean	-18.5908716	-17.7527024
Variance	0.767743926	0.72923662
Observations	13	13
Pearson Correlation	0.990784315	
Hypothesized Mean Difference	0	
df	12	
t Stat	-25.2837035	
P(T<=t) one-tail	4.44916E-12	
t Critical one-tail	1.782287556	
P(T<=t) two-tail	8.89832E-12	
t Critical two-tail	2.17881283	

Appendix 15 continued.

OYSTERS

	Variable 1	*Variable 2*
Mean	-20.86815319	-19.355
Variance	3.125373304	2.17528
Observations	12	12
Pearson Correlation	0.961836721	
Hypothesized Mean Difference	0	
df	11	
t Stat	-9.821121143	
P(T<=t) one-tail	4.4258E-07	
t Critical one-tail	1.795884819	
P(T<=t) two-tail	8.85161E-07	
t Critical two-tail	2.20098516	

Appendix 16: Description of Gelman-Rubin and Geweke diagnostics of Bayesian mixing model indicating convergence and true posterior distribution was met.

##
Gelman-Rubin Diagnostic
##

Generally the Gelman diagnostic should be < 1.05

Out of 61 variables:
0 > 1.01
0 > 1.05
0 > 1.1

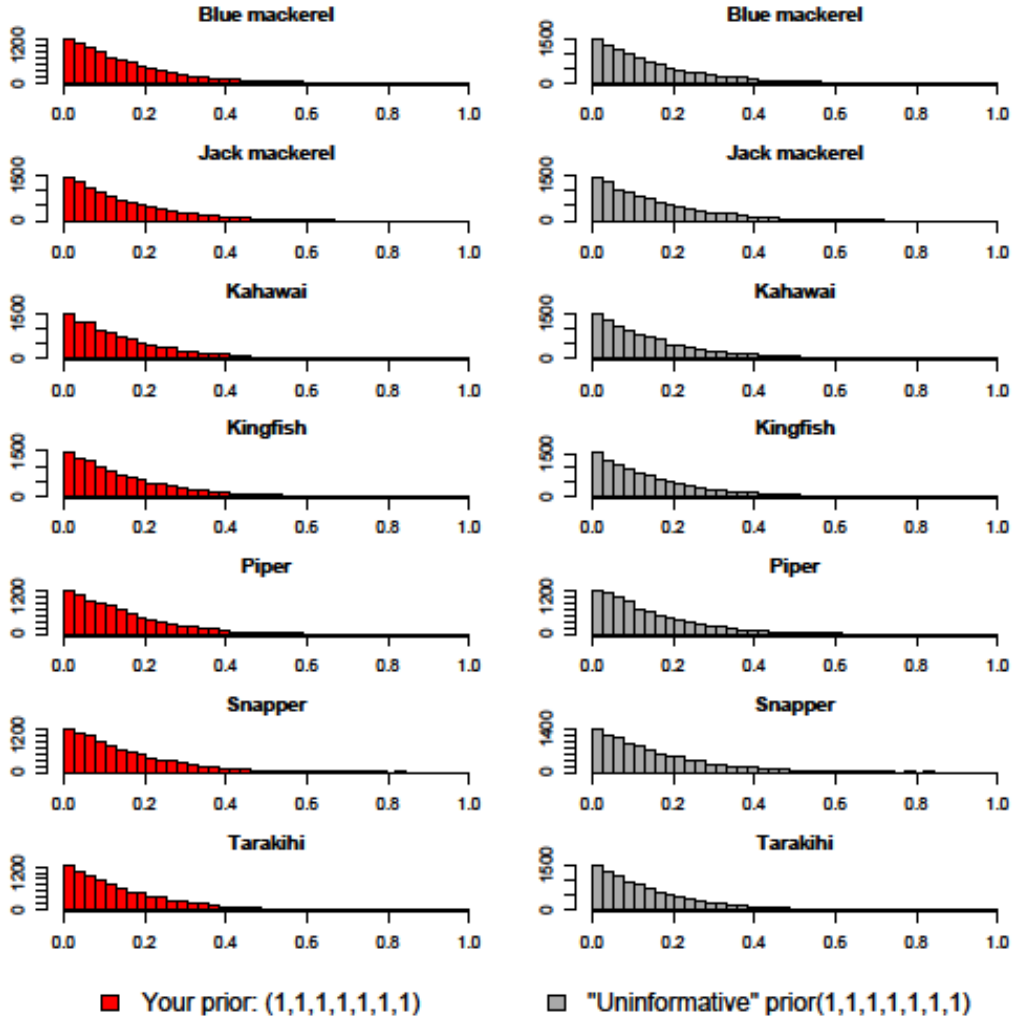
##
Geweke Diagnostic
##

The Geweke diagnostic is a standard z-score, so we'd expect 5% to be outside +/- 1.96

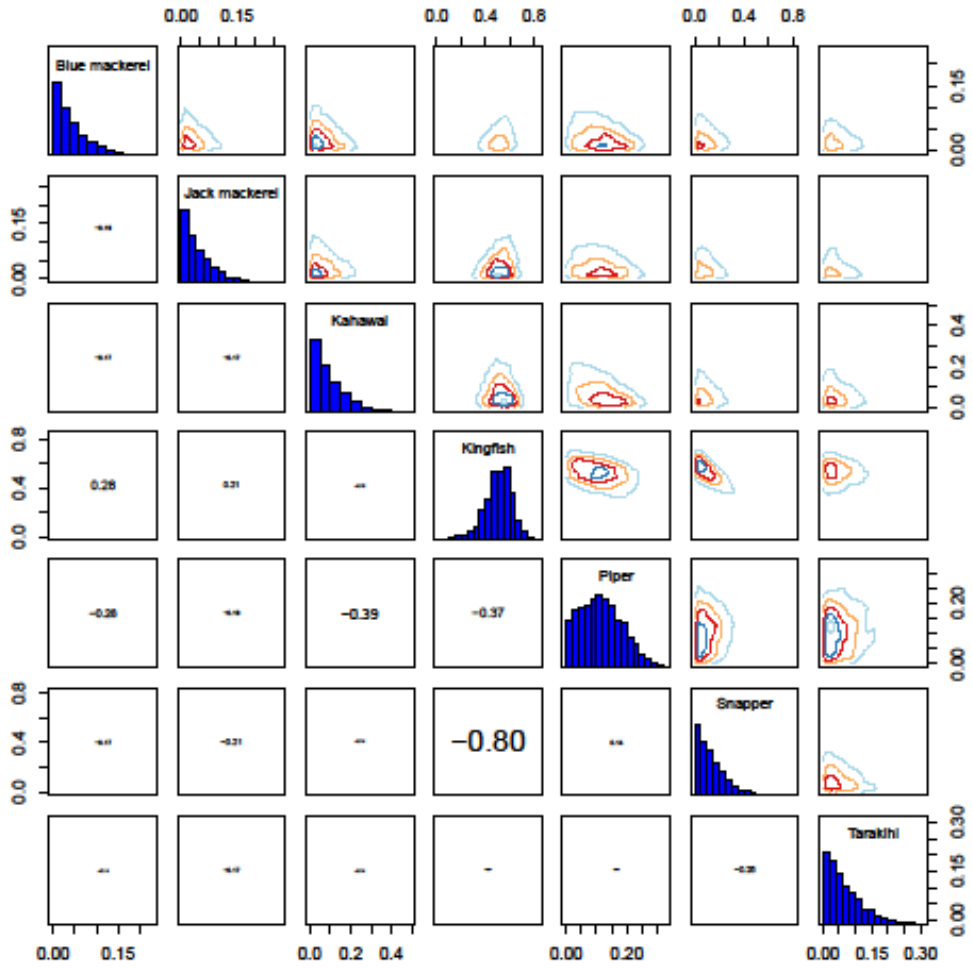
Number of variables outside +/-1.96 in each chain (out of 61):

	Chain 1	Chain 2	Chain 3
Geweke	2	1	2

Appendix 17: Bayesian mixing model prior plot showing uninformative prey contributions to the diet of bronze whaler sharks.



Appendix 18: Bayesian mixing model pairs plot showing proportion of prey contributions to the diet of bronze whaler sharks.



Appendix 19: Graphical representation of putative trophic pyramid of bronze whaler sharks (*Carcharhinus brachyurus*) in the Bay of Plenty, North Island, New Zealand.